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SOME LICHENS OF TROPICAL AFRICA. II. USNEA. (*Continued*)

CARROLL W. DODGE*

1. USNEA CERVICORNIS Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Southern Rhodesia, Makoni Inyanga District, summit of Forrest-Hill Kop, 1700 m., on shaded rock face, *Frederick Eyles 827*, at Kew.

Thallus erect, forming fragile tufts up to 8 cm. tall from a common holdfast, root-like fibers more than 2 mm. long (broken); unbranched or irregularly dichotomous, 2 mm. in diameter, terete, somewhat flattened at the axils, citrine drab shading to olive buff above, not articulate nor inflated; surface areolate, subfoveolate, minutely and irregularly papillate, papillae with black tips mostly broken off, leaving white punctiform scars, the younger portions smooth, irregularly white-reticulate; eramulose.

Apothecia lateral, about 1 cm. below the recurved tip of a branch, 8 mm. in diameter, margin crenate, eciliate or with one to two cilia up to 8 mm. long, about 0.5 mm. in diameter, somewhat inflated in the middle, with obtuse tips; disc epruinose, ochraceous salmon or buffy brown; exciple surface similar to that of the thallus but cortex scarcely areolate and less white-punctate. Cortex fastigiate, 40–65 μ thick, of slender hyphae in a gel, the outer 12 μ deeply staining, heavily nubilated with minute brownish crystals, penetrated by occasional filaments of *Trentepohlia*, moniliform, cells nearly isodiametric, 7–8 μ in diameter, outermost spherical protoplast not uniformly staining (cleavage of zoospores?). Medulla about 65 μ thick, thinning somewhat toward the margin, of loosely woven, thick-walled hyphae about 4 μ in diameter, heavily nubilated with minute hyaline crystals; algal layer under the parathecium about 25–30 μ thick; parathecium hyaline, 40 μ thick, hyphae perpendicular to the surface, thick-walled, slender, conglutinate; hypothecium of slender, somewhat loosely woven periclinal hyphae; thecium 75–

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80 μ tall; paraphyses conglutinate, upper 15 μ heavily nubilated with brown crystals, tips not thickened; asci clavate, 40–45 × 10–12 μ, tips thickened when young; ascospores 8, monostichous, unicellular, about 8 × 4 μ (in ascus probably not quite mature).

Cortex of branch 190–200 μ thick, consisting of an outer layer 40 μ thick, of slender, predominantly radial hyphae so heavily nubilated by brown crystals that structure not clear even in thin sections, and a gelified layer 150–160 μ thick, of hyaline, thick-walled, branched and interwoven hyphae predominantly radial; algal layer about 30 μ thick, of radial filaments of *Trentepohlia*, cylindric, 6–8 μ in diameter, cells nearly isodiametric, sending broad columns of filaments up through the cortex, 25–135 μ thick, forming fracture planes for the areolate cortex; medulla 80–95 μ thick, of thick-walled, branched and interwoven hyphae, so densely nubilated with brown crystals that the structure is obscured; axis hollow, stuffed, 1500 μ in diameter, chondroid cylinder shallowly lacerate on the outside, more so within, 250–300 μ thick, of very thick-walled, interwoven, branched, predominantly longitudinal hyphae, lumen about 1 μ in diameter; cavity 500–750 μ in diameter, loosely stuffed with interwoven, predominantly radial hyphae 5–6 μ in diameter, lumen 1–2 μ, growing out as branches from the axis hyphae.

This species is closest to *U. Liechtensteinii*, with a narrower cavity, ramuli and white-tipped papillae; the apothecia are terminal with a rugulose exciple.

2. USNEA PERHISPIDELLA Steiner, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 106:210. 1897.

Type: Kenya, Machakos, *Liechtenstein & Pospischill.*

Thallus about 6 cm. tall, fruticose, rather rigid, pale grayish green, drying raw umber to antique brown in the herbarium; base thick, slightly fuscous, often giving rise to several branches, rather closely dichotomous, internodes mostly 6–8 mm. long, axils acute to nearly right angles; branches about 2 mm. thick below, about 1.2 mm. thick above, continuous or distinctly annularly cracked, cortex subareolate, areoles plane, terete or only slightly deformed; papillae minute, elongating to short spinulose isidia which soon break away leaving minute pseudocyphelliform scars, often confluent in short rows, more rarely germinating *in situ* as slender pseudoramuli 2–3 mm. long, slightly curved upward; ultimate branches flexuous, slender, tips acute.

Apothecia lateral, then appearing subterminal, sessile, 3–5 (–6) mm. in diameter, concave, cup-shaped, finally subplane; exciple rugose with short spines; marginal cilia rare, subdistant, mostly 2 mm. long, conic, a few up to 10 mm. long with spinules at their base; ascospores 10–13 × 7–8.5 μ in clavate asci.

Cortex up to 80 μ thick, dilacerate, chondroid, fragile, of predominantly periclinal hyphae, the outer 20 μ brownish, deeply staining, almost a thick-walled pseudoparenchyma; algal layer 25–50 μ thick, of radial filaments of *Trentepohlia*,

cells 6–7 × 10–11 μ; medulla 180μ thick, closely woven to subarachnoid, K sulfur-yellow; axis solid, about 360 μ thick.

Only two young plants with a single apothecial initial were found in the material from S. Sudan. The material from Kenya is typical.

S. SUDAN: Issore, Onejiro, 1775 m., corticole, 3° 50′ N., 32° 50′ E., *T. F. Chipp 57*, at Kew.

KENYA: Endabarra-Mau Forest, 2355 m., on *Acacia*, *P. R. O. Bally B4947*, in E. African Herb.

3. USNEA SOREDIOSULA Müll. Arg. in Motyka, Lich. Gen. Usnea Stud. Monog. 330. 1937.

Type: Tanganyika, Usambara, near Kumba marsh, *C. Holst* sub *U. barbata* v. *sorediosula* Müll. Arg. at Genève.

Thallus erect, rigid, fruticose, up to 8 cm. tall, pale ashy, drying deep olive buff from soredia, exposed portions of the axes Isabella color; holdfast conic, black, up to 4 mm. in diameter; base cylindric, 3 mm. tall, about 2 mm. in diameter, annularly cracked; repeatedly, often unequally, dichotomous at acute or right angles, the branches 1.6 mm. in diameter below, more slender at each dichotomy, variously curved and intricate, rarely concrescent, forming a dense tangle broader than tall; terete, indistinctly annularly cracked or subareolate below, smooth above between the low tubercles which are rather close, sometimes in rows or rarely concrescent in short low ridges, soon forming isidiose soredia and appearing farinose as the soredia are dispersed over the whole plant, except less dense over the basal internodes; eramulose; summits up to 20 mm. long, subcapillaceous, rather closely dichotomous but mostly broken off. Apothecia not seen.

Cortex up to 160 μ thick, very densely woven in upper 30 μ, more loosely woven below, imbedded in a yellow gel; algal layer up to 130 μ thick, of radial *Trentepohlia* filaments, cells up to 10 μ long, 6–7 μ in diameter, below forming a continuous layer about 50 μ thick with projections into the cortex up to 80 μ tall and some filaments growing in columns to the surface of the cortex to form the soredia; medulla 65–125 μ thick, very densely woven under the algal layer and next the axis, loosely woven between, hyphae 4–5 μ in diameter, lumen 1 μ, nubilated with brownish crystals; axis 430 μ thick, of interwoven hyphae 3 μ in diameter, lumen 1 μ, conglutinate, predominantly longitudinal.

UGANDA: Kigezi, Kabale River, on trees, 1970 m., *I. R. Dale L1*; Mafuga, 2580 m., *I. R. Dale 42*; Ruizi River, 1390 m., *T. Jarrett 402*; all at Kew.

4. USNEA NUTANS Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Kenya, Northern Frontier Province, Mt. Kulal, 1935 m., on exposed rock, *P. R. O. Bally 5685*, at Kew.

Thallus erect to decumbent, rigid especially below, about 8 cm. tall, cinnamon buff on the main axes shading to dark olive buff on the ultimate branches; holdfast black, hemispheric, 5 mm. in diameter, forming root-like structures below, giving

rise to 10 or more primary axes above; bases below the first dichotomy varying from 1 to 10 mm. long, 1.5–2 mm. in diameter, blackened below; branching variable, dichotomous, at nearly right angles, the branches curving upward with short internodes below, then longer internodes and spreading branches in the mid-portion, more closely branched and the branches recurved above, terete, smooth below with the cortex annularly cracked and subareolate, minutely verrucose above, each verruca bearing a single short isidium, black-tipped, decadent, leaving minute white scars; eramulose; the nodding ultimate branches smooth, minutely black-tipped. Apothecia not seen.

Cortex up to 200 μ thick, cartilaginous, outer 40 μ fastigiate, of slender hyphae heavily nubilated with brownish crystals, the rest of loosely woven, branched and anastomosing hyphae in a gel, in some places penetrated by strands of somewhat disorganized algal filaments from below to a height of 100 μ; algal layer variable in thickness, up to 50 μ, of radial branched filaments of *Trentepohlia* 5–6 μ in diameter, somewhat moniliform, cells 7–8 μ long, apparently not helping to form the cortical cracks as in other species of this section; medulla about 100 μ thick, of densely woven, slender hyphae 3 μ in diameter, heavily nubilated with brownish crystals, tending to tear apart in the middle, allowing areoles to flake off and making sectioning difficult; axis 550–575 μ in diameter, the inner half minutely lacerate, forming many small stuffed cavities, not a single cavity as in most other species.

The habit of our species is reminiscent of a tuft of a species of *Cladina* with recurved tips. It resembles the smaller *U. capensis* somewhat in habit but differs in many macroscopic and microscopic details.

UGANDA: Kigezi, Kabale River, 2260 m., on tree, *I. R. Dale L43*, at Kew.
KENYA: Northern Frontier Province, Mt. Kulal, 1935 m., on exposed rock, *P. R. O. Bally 5686*, type at Kew.

5. USNEA DODOMAE Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Tanganyika, Dodoma Prov., Mt. Mpwapwa, 1610–1935 m., saxicole, *P. J. Greenway 2432*, in East African Herb.

Thallus erect or decumbent in dense tufts, 10 cm. tall, rigid, from a common holdfast, up to 15 mm. in diameter, of dense yellowish, root-like processes at least 3 mm. long, penetrating between the rock crystals; branches about 1.5 mm. thick at the blackened base, expanding to 2 mm. below the first dichotomy, 10–15 mm. above the holdfast; further branching variable from dichotomous to almost sympodial, ultimate branches up to 7 cm. long; flexuous, tapering gradually to the acute tip; eramulose (occasionally the ultimate branches once or twice unequally dichotomous 1–2 cm. from the tip, forming pseudoramuli), light brownish olive shading upward through Isabella color to almost honey yellow at the tips; not articulate nor inflated; cortex cracked and subareolate below, otherwise smooth, densely covered throughout most of the plant with short spinulose isidia which

soon break away leaving minute punctate scars (appearing as pseudocyphellae or when aggregated in short rows on indistinct ridges, giving a slightly foveolate appearance), the ultimate 2 mm. nude of spinules. Apothecia not seen.

Cortex about 180 μ thick, horny, fastigiate above (upper 15 μ), more loosely woven below, all imbedded in a gel; algal layer about 50 μ thick, of more or less radial filaments of *Trentepohlia* 4–5 μ in diameter, cells varying from isodiametric to 8 μ long; medulla 65–70 μ thick, of very densely woven hyphae, nubilated with brown crystals, thick-walled, easily cracking away from the axis in sectioning; axis about 970 μ in diameter, hollow, the walls about 360 μ thick, of very densely woven, thick-walled hyphae in a gel; central cavity somewhat irregular in outline, 250–350 μ in diameter, stuffed with loosely woven brownish hyphae.

TANGANYIKA: Dodoma Prov., Mt. Mpwapwa, 1619–1935 m., saxicole, *P. J. Greenway 2432*, in E. African Herb.

6. USNEA PULVINULATA Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Uganda, Kigezi, Kasatoro forest, 1935–2560 m., on trees, *I. R. Dale L39*, at Kew.

Thallus fruticose, erect, up to 5 cm. tall, between wood brown and deep olive buff (seen from above), the main branches citrine drab, blackening below; holdfast a black verrucose disc about 8 mm. in diameter, the base black, about 4 mm. tall, 2 mm. in diameter; branching dichotomous to sympodial, internodes short, producing a subhemispheric tuft, the ultimate branches about 2 cm. long, 1 mm. in diameter, annularly cracked and subareolate in the lower blackened portion, otherwise smooth but very densely ramulose, the ramuli rather fragile below and the broken bases suggesting papillae, some regenerating as several spinules which probably serve as isidia; the cortex cracking off in patches, exposing the light coral red lower medulla and surface of the axis; ramuli acuminate, 0.5–3 mm. long, straight, axils acute.

Apothecia subterminal, mostly appearing terminal, up to 15 mm. in diameter, cupulate at first, becoming nearly plane; exciple shallowly scrobiculate, closely ramulose along the ridges; marginal cilia crowded, about 2 mm. long, tips acuminate, rather fragile and many broken off in older apothecia; disc smooth to somewhat unequal, densely white-pruinose when young, becoming cinnamon rufous to apricot orange.

Cortex 65–100 μ thick, fastigiate, hyphae 6–7 μ in diameter, lumen 3 μ, the outer 30 μ nubilated with minute brown crystals, gelified, the hyphae less clearly radial in the inner portion; algal layer about 40 μ thick, of predominantly radial filaments of *Trentepohlia*; medulla 30 μ thick, of coarse periclinal hyphae 6–7 μ in diameter, relatively thin-walled; axis 1550 μ in diameter, hollow, the wall 270 μ thick, of longitudinal hyphae 6 μ in diameter, lumen 2–3 μ, cavity 1100 μ in diameter, stuffed with branched brown, thick-walled hyphae, 6–7 μ in diameter, growing out of the wall.

In habit, this species suggests the DENSIROSTRAE, the hollow axis and red lower medulla suggest the subgenus EUMITRIA, although the presence of *Trentepohlia* algae clearly place it in the ROCCELLINAE.

UGANDA: Kigezi, Kasatoro forest, 1935–2560 m., on trees, *I. R. Dale L39*, at Kew.

7. USNEA LIECHTENSTEINII Steiner, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 106:211. 1897.

Type: Kenya, Machakos, *Liechtenstein & Poppischill*, saxicole.

Thallus 5–10 cm. tall, erect, caespitose, fruticose, rigid, citrine drab to deep olive buff, becoming brownish olive to Isabella color; holdfast blackened, sending root-like fibers about 0.5 mm. in diameter between the rock crystals, furnishing a common base for many primary axes; lower joint 5–10 mm. long, 1.5 mm. in diameter at the base, expanding upward to 2 mm. in diameter at the first dichotomy, several times dichotomous with very short internodes, then less frequently and irregularly so above; terete, cortex areolate, the areoles slightly foveolate below, then closely verrucose and subpapillate above, the verrucae sometimes in close rows but never distinctly angled, tips white but not perforate nor sorediate; ramuli irregularly disposed, thick, curving upward and subappressed, mostly 4–5 mm. long, nearly smooth, rather fragile and the obtuse tips often broken off.

Apothecia lateral, about 1 cm. back of the tips of the smaller branches, cupulate, 5–7 (–10) mm. in diameter; exciple smooth at first, becoming reticulate-rugose in relatively large areoles at maturity; marginal cilia erect, not dense, about 3 mm. long, then more spreading and annularly cracked, especially at the base, and often broken off at maturity; disc epruinose, buffy brown.

Cortex gelified, about 275 μ thick, the outer 25 μ obscured by brownish crystals, the hyphae thick-walled, branched and anastomosing but predominantly radial, 2.5–3 μ in diameter; algal layer about 50 μ thick, of *Trentepohlia* filaments, mostly radial, about 6 μ in diameter, cells cylindric, somewhat longer than broad, penetrating the cortex in bands and forming fracture planes between the areoles of the cortex; medulla 50–80 μ thick, of slender, very densely woven hyphae, heavily nubilated with minute brownish crystals, axis 750 μ in diameter, hollow, wall 250–300 μ thick, of very thick-walled, densely woven hyphae in a gel; cavity about 125–150 μ in diameter, irregular in outline, more or less stuffed with medullary hyphae which grow through the axis wall in radial strands about 150 μ wide, analogous to the rays of woody stems of flowering plants and perhaps performing the same functions.

TANGANYIKA: Dodoma Prov., Mt. Mpwapwa, 1610–1935 m., saxicole, *P. J. Greenway 2432*, at Kew; *2432a* in E. African Herb. (separated from the collection of *U. Dodomae* Dodge).

8. USNEA SUBCRISTATA Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Tanganyika, Kondoa District, Swaga-swaga Hill, summit, 1775 m., on shrubs, chiefly *Tricalysia cacondensis*, *B. D. Burtt 891*, at Kew.

Thallus erect, very rigid, fruticose, 7–8 cm. tall, light brownish olive below, shading through Isabella color and honey yellow to chamois on the slender branches and ramuli, the upper ends of branches between chamois and deep olive buff; base and first branchings not seen as the plant has been glued to the herbarium sheet, and are obscured by several layers of branches; branch 7 cm. long, 2 mm. in diameter at its base, expanding to 3 mm. at the first lateral branch and then tapering slowly to about 1 mm. in diameter below the apothecium, rather densely ramulose, nearly terete in the lower two internodes; cortex subareolate, then coarsely papillate above, the papillae in predominantly longitudinal rows, making the branch angled, some of the papillae growing out to form ramuli; larger lateral branches similar to the main axis but 1–1.5 mm. in diameter; ramuli 1–15 mm. long, thick, tips rounded, the larger foveolate, the smaller nearly smooth; some of the larger ramuli may develop into slender lateral branches 0.4–0.5 mm. in diameter, sparsely papillate below, foveolate above, tips rounded.

Apothecia apparently terminal, nearly plane, up to 20 mm. in diameter; exciple smooth or papillate with radial ridges (as many as there are ridges at the top of the branch), smooth between; marginal cilia 2-ranked, subdistant, the outer rank coarse, often dichotomous above the base, tips acute, otherwise resembling larger ramuli, the inner rank slender, 1–2 mm. long, tips acute; disc vinaceous buff, or pale olive buff, pruinose.

Cortex variable in thickness, 50–90 μ, fastigiate, highly gelified, the outer 10 μ deeply staining; algal layer dentate outward, up to 40 μ thick, cells 6–7 μ in diameter, closely packed, protococcoid; medulla K—, about 130 μ thick, brownish, of densely woven hyphae with a narrow zone of loosely woven hyphae in the middle; axis 1400 μ thick, hollow, wall 300 μ thick, of longitudinal conglutinate thick-walled hyphae; cavity about 800 μ in diameter, more or less lined with a layer of thin-walled hyphae 10 μ in diameter, with deep brown contents; very loosely stuffed with hyaline thin-walled hyphae 5 μ in diameter, nubilated with hyaline crystals and a few hyphae similar to those lining the cavity.

This fertile highland species differs from the lowland, sorediose *U. cristata* in being a coarser plant with more but less sharply defined angles on the main axis and larger branches and in the more abundant, larger and subfoveolate ramuli.

9. USNEA ELATA Motyka, Lich. Gen. Usnea Stud. Monog. 57. 1936.

Type: Congo; M'pala, west shore of Lake Tanganyika, *Guillemé*.

Thallus 20 cm. long, probably erect, rather rigid, buffy olive to ecru olive; holdfast a coarsely verrucose disc 5–6 mm. in diameter, dark brown, giving rise to one or more main axes 2 mm. in diameter, with many small, short branches in the

lowest cm., then repeatedly dichotomous in the lower half, internodes about 1 cm. long, thinning at each dichotomy, axils complanate, nearly 90° angles, the branches soon erect before the next dichotomy, the internodes subterete to few-angled from low longitudinal or suboblique ridges, cracked and minutely isidiose, appearing farinose after the isidia are shed; in the upper two-thirds the ridges more irregular and anastomosing, giving a foveate appearance with minute isidiose verrucae between, the internodes more variable in length, some very short, giving a trichotomous appearance, others very long; summits long-capillaceous, rather fragile and broken off in our plants; eramulose (occasionally isidia grow out *in situ* forming groups of pseudoramuli 1–2 mm. long) or the small branches on the basal internode produce larger pseudoramuli from unequal dichotomies.

Apothecia rather rare, about 5 mm. in diameter, cupulate, sessile on the larger axes; exciple smooth to slightly impressed; marginal cilia moderately close, erect, variable in length up to 4 mm. long, the longer dichotomous near the tips, sparsely and minutely verrucose, perhaps finally isidiose; disc flesh color with a white pruina.

Cortex variable in thickness, 50–85 (–150) μ thick, gelified, loosely fastigiate, the outer 15 μ very dark brown; algal layer 30–50 μ thick, of discrete colonies of *Trebouxia,* cells 4–7 μ in diameter, forming a nearly continuous layer; medulla pink to rose color, I—, about 240 μ thick, quite closely woven next the algal layer, looser below (appearing dense under low magnification), hyphae 3–4 μ in diameter, lumen 1 μ; axis 840 μ in diameter, deep rose by reflected light, hyaline by transmitted light, slightly irregular in transverse section, wall about 200 μ thick, but cavity very irregular in outline (radiating sinuses), from the coalescence of many small cavities, about 30 μ in diameter, lined with larger thin-walled brownish hyphae, nearly hollow but traversed by an occasional hyaline hypha 6 μ in diameter, lumen 3 μ; wall hyphae longitudinal, very thick-walled, conglutinate, I slightly blue, especially next the cavity.

KENYA: Lake Ngunga, 1775 m., on trees, *G. M. Allen 1782,* in Howe herb. at Farlow Herb.

10. USNEA NANA Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Uganda, Kigezi, Kasatoro, Kabale River, 2256 m., corticole, *I. R. Dale L43 p. p. min.*

Thallus fruticose, erect, up to 4 cm. tall, deep olive to citrine drab; holdfast 2 mm. in diameter, conical, black, base 3–5 mm. tall, up to 1 mm. in diameter, black; once or twice dichotomous at the base, rarely dichotomous above; axes terete, up to 1 mm. in diameter below, tapering upward, smooth, densely ramulose, ramuli 1–2 mm. long, axils acute, tapering to a slender, obtuse, not blackened tip, not fragile, a few up to 4 mm. long, curved, rarely once-dichotomous; summits tapering to an acute tip, nude of ramuli in the upper 4 mm.

Apothecia sessile on the lower portions, of small secondary branches, cupulate, 1 (–2) mm. in diameter; exciple smooth; marginal cilia close, radiating, 1 mm. long,

resembling small ramuli but more fragile; disc concave, flesh color, white-pruinose.

Cortex 35–40 μ thick, of coarse conglutinate thick-walled predominantly radial hyphae 8 μ in diameter, lumen 3 μ (in places appearing pseudoparenchymatous); algae *Trebouxia*, in colonies 20–30 μ in diameter, in a nearly continuous layer, cells 7–8 μ in diameter; medulla up to 15 μ thick, of compact, periclinal thick-walled hyphae 3 μ in diameter; axis 800 μ in diameter, hollow, wall 150 μ thick, of slender thick-walled conglutinate hyphae; cavity 500 μ in diameter, very loosely stuffed with very thick-walled hyphae 3 μ in diameter.

11. USNEA FIRMULA (Stirton) Motyka, Lich. Gen. Usnea Stud. Monog. 64. 1936.

Eumitria firmula Stirton, Scottish Nat. 6:100. 1881.

Type: Fernando Po, lava beds, *G. Thomson*, in the Art Galleries of the Glasgow Corporation.

Thallus about 10 cm. tall, rigid, ashy green, sparingly branched, closely ramulose; branches straight to somewhat flexuous, terete, 1–2 mm. in diameter, tapering somewhat above and below, thus appearing somewhat inflated, verrucose-papillate between the ramuli (perhaps only very young ramuli or scars of broken ramuli regenerating); main axes and bases of slender lateral branches densely ramulose, ramuli 5–15 mm. long, perpendicular, straight or slightly flexuous and arcuate, mostly annularly cracked at the base showing the rose medulla, tips slender but obtuse, not very fragile, breaking off near the tips; summits of slender lateral branches nude with abundant low white tubercles in our plants.

Apothecia terminal on lateral branches, 7–10 (–15) mm. in diameter, nearly plane; exciple convex, papillose, sometimes ciliate; marginal cilia rare, 5 mm. long, smooth; disc nearly plane, pale flesh color with a white pruina; epithecium dark; ascospores 8 × 10 μ, in narrow asci.

Migeod 419 is very old; the apical portions of most of the main axes are broken off, carrying away the apothecia. The color is between buffy brown and citrine drab rather than ashy green. The axis is black under the rose-colored medullar surface. It agrees in vegetative characters better with this species than with the sterile sorediose *U. implicita* (Stirton) Zahlbr. from the same region. The low white tubercles on the apical portions of the slender lateral branches may be initials of soralia but are not found on the main axes as are the soralia of *U. implicita*. *Dale L43* seems to be the juvenile stage of this species: It is only 3 cm. tall, the axis still solid, the medulla only partly rose color. It is sorediose and beginning to form an apothecium less than a mm. in diameter.

CAMEROONS: gully above Bamenda, 1930 m., *F. W. H. Migeod 419;* Cameroon Mt., 1610 m., *Dunlap;* above Buea, 1450 m., *F. W. H. Migeod 144;* all at Kew; *Bornmueller* misit Zahlbruckner sub *U. Baileyi*, in Howe herb., at Farlow Herb.

FERNANDO PO: lava beds, *G. Thomson*, type, in the Art Galleries of the Glasgow Corporation.

S. SUDAN: Onyiro, Issore, 1775 m., 3° 50′ N., 32° 50′ E., *T. F. Chipp 57*, at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., on tree, very young, *I. R. Dale L43;* Bwamba Pass, 2250 m., on trees, *E. M. Shillito 90a;* both at Kew.

12. USNEA MEDIO-AFRICANA Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Uganda, Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.

Thallus erect, subrigid, about 5 cm. tall; common holdfast about 7 mm. in diameter, flat, black, giving rise to 4–5 primary axes about 1.5 mm. in diameter; base very short, once or twice dichotomous with very short internodes and again dichotomous less than 1 cm. from the apothecia, mummy brown with dark olive buff ramuli; terete to slightly rugose, angular and subfoveolate; ramuli dense, 5–7 mm. long, very fragile and mostly broken off, the scars giving a coarsely verrucose to papillate appearance, smooth, annularly cracked, tips acute and minutely blackened.

Apothecia subterminal, up to 20 mm. in diameter, plane; exciple foveate, minutely verrucose, with radial ridges from concrescent ramuli; marginal cilia rather close, of variable length, up to 8 mm. long, the larger once dichotomous or sparsely ramulose; disc cinnamon, very slightly white-pruinose.

Cortex 60 (–100) μ thick, of predominantly radial, loosely woven slender hyphae in a gel, the outer 15 μ more densely woven and deeply staining; algal layer continuous, about 30 μ thick, of closely packed protococcoid cells; medulla 40 (–180) μ thick, white, pale rose next the axis, of very loosely woven, slender, thick-walled hyphae, more densely woven next the algal layer and the axis; axis 900 μ in diameter, solid at first becoming hollow, wall 180 μ thick, of slender conglutinate hyphae, cavity 550 μ in diameter, stuffed at first then hollow.

In sectioning the mature primary axes, the cortex and algal layer tear away from a thin layer of medulla next the axis, making it impossible to estimate the thickness of the mature medulla accurately. In *Hendrickx 4330* the medulla is 30–35 μ thick, compactly woven throughout.

This species is closest to *U. trullifera* Nyl. of Motyka's monograph and perhaps the atypical specimen cited by him from Tanganyika?. Mt. Mfimbwa, near Lake "Tanganyika-Nyassa", 2300 m., *From*, belongs here. Our plants differ from the Tahitian plants in being smaller with much larger apothecia and relatively thicker medulla.

UGANDA: Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.
CONGO: km. 30, route Kahusi, ramulicole, *F. L. Hendrickx 4330*, in E. African Herb.

13. USNEA BRUNNESCENS Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Uganda, Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.

Thallus at least 10 cm. tall, fruticose, rather rigid, drying Mars brown to russet on the axes, younger ramuli cinnamon buff; holdfast a black disc about 7 mm. in diameter, giving rise to at least three branches, twice or thrice dichotomous with short internodes (1 cm. or less), then rarely dichotomous above, about 2 mm. in diameter in the lower half, then tapering to about 0.3 mm. at the densely ramulose blunt tip; cortex impressed and subareolate, nearly smooth in the lower internodes,

then very densely verrucose-papillate and ramulose above; ramuli 1–3 mm. long, single or in short oblique rows, but the branches not clearly angled, annularly cracked at the base and often the tips broken off, but seldom breaking away at the base to leave scars, the larger ramuli sparsely verrucose, producing single isidia on the verrucae, but not sorediate.

The tips of the branches end in a dense cluster of ramuli, perhaps a regeneration phenomenon following the breaking off of the end of the branch.

Cortex about 50 μ thick, of loosely woven, predominantly radial, slender hyphae in a gel, the outer half nubilated with minute hyaline crystals; algal layer about 40 μ thick, a nearly continuous layer of *Trebouxia* colonies, cells about 6 μ in diameter; medulla about 30 (–40) μ thick, of slender, very densely woven hyphae; axis about 1400 μ in diameter, hollow, wall 135 μ thick, of longitudinal, thick-walled conglutinate hyphae, lumen about 2 μ in diameter, cavity loosely stuffed with branched, anastomosing thick-walled hyphae up to 4 μ in diameter.

UGANDA: Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.

14. USNEA VERSICOLOR Motyka, Lich. Gen. Usnea Stud. Monog. 74. 1936.

Type: Cameroons, Cameroon Mt., 4040–4070 m., on volcanic ash, *Weberbauer*.

Thallus prostrate or subpendent, 20–30 cm. long, larger joints clay color to cinnamon buff, others light brownish olive, slender branches deep olive buff, base not seen, subarticulate, branching subdichotomous, the larger branch continuous at the axil, the smaller articulate and constricted, cracks narrow, dividing into joints not constricted at the ends but slightly inflated in the middle, somewhat flexuous, surface very slightly and indefinitely foveolate, with small round pseudocyphellae, or short, oblong, scarcely elevated farinose longitudinal ridges; main axes up to 1.5 mm. in diameter below, tapering above to the capillaceous summits; eramulose but the more closely dichotomous, very slender branches of the summits may simulate ramuli.

Our material from the same mountain at approximately the same elevation agrees well with Motyka's description except for the presence of inconspicuous pseudocyphellae and farinose ridges. As our plants are somewhat longer, perhaps they are older and these structures more developed. This species seems intermediate between the FOVEATAE and the ARTICULATAE.

CAMEROONS: Cameroon Mt., 4030 m., on bare rocky ground, *F. W. H. Migeod 196*, at Kew.

15. USNEA COMPLANATA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 109. 1936.

Usnea barbata v. *strigosa* f. *complanata* Müll. Arg., Hedwigia 31:276. 1892.
Usnea florida v. *strigosa* f. *complanata* Zahlbr., Cat. Lich. Univ. 6:574. 1930.
Usnea florida v. *strigosa* f. *pygmaea* Hue, Nouv. Arch. Mus. Paris IV. 1:35. 1899.
Usnea Schimperi Lenormand, herb. nom.

Type: Ethiopia, Debr; Eski, 2900 m., on trunks of *Euphorbia Collqual. W. Schimper*, 1852. The type of *U. florida* v. *strigosa* f. *pygmaea* Hue is: Ethiopia, Nahia in Machiha, 1930–2250 m., on *Euphorbia Collqual, W. Schimper 1022*, Nov. 1852.

Thallus erect, up to 3 cm. tall (only 1 cm. tall in our plants), snuff brown to Sayal brown; holdfast hemispheric, verrucose, 5 mm. in diameter, giving rise to several axes varying from nearly terete and foveolate, 2 mm. in diameter, to quite flat, 5 mm. wide, and deeply scrobiculate (resembling a small *Ramalina*), with 1–3 short flat secondary branches, rather densely ramulose in places, nearly nude in others, ramuli infundibuliform at the base, inflated and abruptly narrowed to an acuminate tip, 1–2 mm. long.

Apothecia up to 15 mm. in diameter, terminal, somewhat excentric; exciple foveate with sparse ramuli, some terete, some flattened; marginal cilia rather close, about 2 mm. long, resembling ramuli; disc somewhat concave, flesh color with a white pruina.

ETHIOPIA: M. Bachit, 2400 m., *W. Schimper 14*, ex herb Sbarbaro sub *U. Schimperi* Lenormand, at Farlow Herb. (duplicate cited by Motyka).

16. USNEA CORRUGATA Motyka, Lich. Gen. Usnea Stud. Monog. 105. 1936.

Type: Ethiopia, Podopolani, on *Euphorbia, Schweinfurth*, 1894.

Thallus subpendulous, up to 12 cm. tall, subrigid, brownish olive with ramuli and more slender branches partly buffy olive, very rarely dark red-maculate; base about 5 mm. tall, 2 mm. in diameter, expanding below into an irregular disc; holdfast 4 mm. in diameter, densely sympodially branched just above the base, axils only slightly flattened; branches perpendicular or nearly so, curving apically, secondary branches 10–15 mm. long, nearly 2 mm. in diameter, then trichotomous with greatly flattened axils, then more closely dichotomous or irregularly branched, the branches about 1 mm. in diameter, upper ones 0.5 mm. or less, deeply foveate throughout, the larger rugi longitudinal, acute, bearing dense pale greenish isidiose soredia; ramuli very irregular, often in dense groups on the smaller branches (perhaps from isidia germinating *in situ*), the longer ramuli branched, subarticulate and inflated; summits quite closely divergently branched, tips obtuse. Apothecia not seen.

UGANDA: Kigezi, Kabale, 1960 m., corticole, *I. R. Dale L1*, at Kew.

17. USNEA PULVERULENTA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 107. 1936.

Usnea barbata v. *pulverulenta* Müll. Arg., Flora 68:499. 1885.

Usnea florida v. *pulverulenta* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 1888/89: 1945. 1890.

Type: Ethiopia, Bagla, 2410 m., *Hildebrandt*, 1885.

Thallus fruticose to subpendent, over 6 cm. long (only 4 cm. in our plants), rather flaccid, axis wood brown, ramuli deep olive buff; holdfast a verrucose brownish disc 2 mm. in diameter, base 1 mm. tall, 1 mm. in diameter; dichotomous with internodes 5 mm. long below, 1 mm. in diameter, terete, smooth between the rather dense ramuli, tuberculate to subpapillate above, thinning at each dichotomy, with granular farinose soralia, subfoveolate between, ultimate branches slender, acuminate but rather short; ramuli dense throughout, mostly about 2 mm. long, some 3–5 mm., probably small secondary branches, tuberculate and sparsely ramulose, slightly inflated, tips acute.

Cortex 80 μ thick, gelified, fastigiate, almost pseudoparenchymatous, cells about 4 μ in diameter, 6–7 μ long, rather thin-walled below, thicker-walled above with very narrow lumina; algal layer 20–35 μ thick, of *Trebouxia*, cells 7–10 μ in diameter, somewhat angular from mutual pressure; medulla about 225 μ thick, the outer half of densely woven predominantly periclinal hyphae, the inner half of predominantly radial, very loosely woven hyphae about 4 μ in diameter, sparsely nubilated with hyaline granules, K— or faintly yellow (the axis tears loose from this inner zone in sectioning, making measurement of the thickness of the medulla inexact); axis 350 μ in diameter, of conglutinate predominantly longitudinal thick-walled hyphae.

Although placed by Motyka in the FOVEATAE, it might equally well be placed in the GLABRATAE, PYCNOCLADAE, near *U. ruwenzoriana* Motyka, as the branches are not, or only very slightly, foveolate above, and the color becomes fuscous in the herbarium; the branches are more densely ramulose than is usual in the FOVEATAE.

ETHIOPIA: Bagla, 2410 m., *Hildebrandt*, 1872, ex herb. Sbarbaro at Farlow Herb.

18. USNEA FLAVESCENS Motyka, Lich. Gen. Usnea Stud. Monog. 125. 1936.

Type: Kenya, Ngongo Bagas, 2700 m., *A. G. Allan*.

Thallus pendent, flaccid, up to 60 cm. long, pale olive buff (in our material), finally becoming pale stramineo-fuscous (*fide* Motyka); holdfast short-conic, black, base slender, about 10 mm. long, 0.8–1 mm. in diameter, 3- to 4-annulate, then more or less frequently dichotomous, often unequally so throughout, articulate, the joints 6–30 mm. long, constricted at the ends, cracks narrow, partly slightly foveate, abundantly so on some joints, very rarely so on others, cortical cracks (pseudocyphellae) rare, inconspicuous, increasing rapidly to 2–2.5 mm. in diameter and decreasing slowly to the almost non-articulate, capillaceous summits; the larger branches somewhat flexuous, sparingly ramulose, sometimes several consecutive joints eramulose; the smaller branches more closely ramulose (imitating a small *U. longissima*); the ramuli of the larger branches up to 1 cm. long, sometimes branched and spinulose; the ramuli of the smaller branches 1–2 mm. long, usually articulate at the base, tips acute and sometimes blackened.

Apothecia sessile on small secondary branches, 2–2.5 mm. in diameter, plane; exciple shallowly foveate; marginal cilia in two ranks, the inner rather close, 1–2

mm. long, suberect, the outer rank subdistant, 3–4 mm. long; disc flesh color, slightly white-pruinose (based on *Curtis 669* from Kenya).

Greenway 3816 is a mixture of several species. On one of the two sheets at the E. African Herbarium is a single plant which seems to be this species, but the color is now (after 21 years) between snuff brown and Sayal brown throughout; some of the joints are very foveate; ramuli more abundant on the larger joints and less so on the capillaceous summits, most of which have been broken off in collecting.

ERITREA: Habab, Tsertsera, *F. Gallina*, ex herb. Cufino at Farlow Herb.
ETHIOPIA: Simien, Mindigabsa, ramulicole, *H. Scott 323*, at Kew.
KENYA: Mt. Kenya, 2250–2575 m., on bamboo twigs, *G. M. Allen 1797*, in Howe and Riddle herbs.; trail from West Kenya Forest Station to summit of Mt. Kenya, 3630 m., *Edgar A. Mearns 1522* (T. Roosevelt Exp.); 40 miles southeast of Narok, 2250 m., *Anita Grosvenor Curtis 669*; all at Farlow Herb.
TANGANYIKA: Kilimanjaro, Bismarck Hill, 3220 m., *P. J. Greenway 3816 p. p. min.*, in E. African Herb.

19. USNEA PRAELONGA Stirton, Scottish Nat. 6:107. 1881.

Type: South Africa, without locality, *J. H. McLea*, in Brit. Mus.

Thallus pendent, flaccid, up to 60 cm. long, gray to yellowish gray, drying dark olive buff to deep olive buff or colonial buff in recent collections to chamois in older collections (Isabella color in the type), lighter on the capillaceous summits; densely dichotomous at the holdfast, branches about 0.5 mm. in diameter, scarcely inflated in the lowest cm., then articulate, joints 5 (–10) mm. long, 2 (–3) mm. in diameter, then sparingly and irregularly dichotomous for the next 30 cm., then repeatedly dichotomous, the joints abruptly more slender and almost cylindric, rather densely dichotomous at the summits; eramulose or very rarely ramulose in the capillaceous summits; surface smooth to somewhat impressed or foveate on the larger joints, pseudocyphellae very inconspicuous, scarcely visible under 10 × magnification, the slender branches minutely foveate with the cortex cracking along the ridges. No apothecia nor soredia seen.

Associated on the sheet of *Gillett 4708* are evidently juvenile plants, the joints not inflated, the surface more foveolate, resembling the smaller branches of the larger plants. *Glover & Gilliland 476* are shorter plants, tawny olive to clay color (collected in 1944), but they seem to be this species rather than *U. articulata* v. *Kotschyana* Motyka from Syria, which they resemble in color.

In the Eritrea to Somaliland region, this species seems confined to *Juniperus*, and the Somalis consider it a part of the juniper tree, it is so constantly associated. The natives use it as a stuffing for pillows and beds. The Ishaak tribes call it *sarokh* or *jeban*.

ERITREA: Filfa forest, *P. E. Ellis 5*, at Kew.
SOMALIE FRANÇAISE: Dai, 1450 m., *G. Popov 1296* (Desert Locust Survey).
BRITISH SOMALILAND: without locality, *R. S Taylor*, Aug. 1927; Libah Mts., Wawanak Peak, 1900 m., 10° 20′ N., 43° E., *J. B. Gillett 4708* (Abyssinia-Somaliland Bound. Comm.); Surud Range, Shimba Beris, 10° 45′ N., 47° 12′ E., *Collenette 402*; Wagar Range, Taisaiver mist belt, *P. E. Glover & H. B. Gilliland 476*; all at Kew.
SOUTH AFRICA: without locality, *J. H. McLea*, type, in Brit. Mus.

20. USNEA PSEUDOCYPHELLATA Motyka, Lich. Gen. Usnea Stud. Monog. 125. 1936.

Type: Cameroons, Buea (Bula in Motyka, *lapsus?*), on old trees, *Deistel.*

Thallus pendent, flaccid, up to 40 cm. long, tawny olive to pinkish buff, summits deep olive buff; base about 5 mm. long, 0.6 mm. in diameter, narrowly blackened below, repeatedly dichotomous in the lower 2 cm., then less so until the capillaceous 7–8 cm., where the internodes are again short; articulate, flexuous, joints 0.3–20 mm. long, mostly about 10 mm. and up to 2 mm. in diameter throughout, tapering only slightly apically and narrowing abruptly to 0.5 mm. or less at the capillaceous summits, constricted at the ends; surface impressed or subfoveolate, pseudocyphellae rare, punctate or in short, very low ridges on the main axes, more abundant and elevated on the smaller secondary branches, farinose, white to pale yellow; ramuli rare, slender, up to 10 mm. long on the main axes, apparently from unequal dichotomies on the capillaceous summits.

Apothecia lateral, 5 (–10) mm. in diameter, cupulate, becoming plane; exciple smooth or with a few periclinal cracks near the margin; marginal cilia few, up to 20 mm. long, slender, subtuberculate with pseudocyphellae; disc chalky white, pruinose, becoming carneous as the pruina weathers away.

SIERRA LEONE: without locality or collector at Kew. Evidently a very old specimen, Verona brown with tawny olive summits, sterile with somewhat shorter joints. In habit it resembles *U. atlantica* Motyka from the Canary Islands, which is said to remain pale stramineous in the herbarium. Motyka cites a specimen from the Canary Islands collected by Humboldt sub *Lichen hirtus* v. *Pini* which must have been over a century old.

CAMEROONS: Mt. Cameroon, 1610 m., *Dunlap*; above Buea, 1290 m. and 1450 m., *F. W. H. Migeod 53, 144* respectively, at Kew.

21. USNEA SPECIOSA Motyka, Lich. Gen. Usnea Stud. Monog. 124. 1936.

Type: Ilha São Thomé, 1300–2100 m., *A. F. Möller.*

Thallus pendent, rather rigid, up to 30 cm. long, drying pale ashy fuscous (Motyka, in our material VanDyke brown to Sayal brown [Fernando Po], tawny olive [Cameroons]); base 3 mm. long, 0.5 mm. in diameter below, expanding upward; dichotomously or sympodially branched once or twice with short internodes, then rarely dichotomous; articulate, joints up to 7 cm. long, 2–2.5 m. in diameter (only 1 mm. in diameter in specimen from 2900 m.), curved to falcate, sharply constricted at the ends, but cortex often continuous; terete, cortex with short, longitudinal or somewhat oblique cracks, farinose, mostly pale sulfur yellow, foveolate, with small punctate pseudocyphellae, not elevated; ramuli occasional on the secondary branches, very rare on the main axes (perhaps only an undeveloped secondary branch); summits abruptly capillaceous, branches 0.4–0.5 mm. in diameter, tapering distally, rather densely dichotomously branched.

Melliss 21, from St. Helena, is apparently the basal portion of an old specimen, about 10 cm. long, hazel to russet with elevated farinose soredia. After years in

the herbarium it has stained the paper to which it is glued, testaceous.

SIERRA LEONE: Loma Mts., Galerie Forest, 1800 m., on *Tridactyla*, *P. Jaeger 4283*, at Kew.

CAMEROONS: Buea, Musaka swamp, 1610 m., *T. D. M. 696*; Victoria, Meyer Crater, 2575 m., *T. D. M. 917*; both at Kew, ex Hb. Bot. Gard. Victoria, Cameroons.

FERNANDO PO: 640 m., 1610 m. and 2900 m., *Gustavo Mann*; all at Kew.

ST. HELENA: without locality, *J. C. Melliss 21*, at Kew.

22. USNEA VESICULATA Motyka, Lich. Gen. Usnea Stud. Monog. 114. 1936.

Type: Tanganyika, R. Uusoro [Wusiro?], in swamp, 2600–3000 m., *Stuhlmann*.

Thallus pendent, up to 60 cm. long, flaccid, main axes drying buckthorn brown to yellow ochre, capillaceous summits between chamois and deep olive buff; holdfast of rooting fibers, repeatedly dichotomous at the top, then sparingly dichotomous on the main axes, thinning at each dichotomy and again closely dichotomous at the base of the capillaceous summits; articulate, joints inflated, 2 mm. in diameter, 10–20 mm. long below, shorter on the main axes above, the capillaceous summits nearly cylindric, but the cortex annularly cracked; surface smooth to impressed or foveate on the larger joints, pseudocyphellae punctate or oblong, farinose, very inconspicuous; eramulose on the main axes, sparingly and irregularly ramulose on the summits, ramuli slender, up to 2 mm. long, often black-tipped.

Apothecia infrequent, not seen in our material, lateral on slender branches, rarely subterminal, 2–4 mm. in diameter, thin, plane; exciple lacunose, marginal cilia few but comparatively long, capillaceous; disc plane, flesh color, slightly pruinose, thecium 60 μ tall; asci narrow; ascospores uniseriate, 10 $\times$ 11 μ, with a distinct epispore.

The material referred here is not uniform. Sometimes a collection, or plants separated from the same collector's number, are much darker, russet to Dresden brown, and the joints of the main axes only about 1 mm. in diameter, surface less impressed and foveate, pseudocyphellae in very low verrucae (visible with 12$\times$ magnification). More field work will be necessary to decide whether they may belong to a different species. In the following list of specimens, they are marked with an asterisk (*) preceding

KENYA: Longondoti, crater forest, 2575 m., arboricole, *R. A. Dummer 5308*, at Kew.

UGANDA: Bugishu, Butandiga, 2415 m., *A. S. Thomas 484*; Elgon Madangi, 3550 m., *A. S. Thomas 607*; Kigezi, * Kasatoro, Kabale River, 2250 m., *I. R. Dale L43*; Mt. Mgahinga, 3380 m., *A. S. Thomas 2457* (both forms); Mafuga, 2575 m., *I. R. Dale L42*; all at Kew.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4300, 4305, 4316*; km. 30, route Kahusi, *F. L. Hendrickx 4330*, a fragment; all in E. African Herb.

ANGOLA: Cuanza Sul, Amboina, Capir near the Carloaongo River, *J. Gossweiler 9991 p. p. min.*, juvenile, at Kew.

TANGANYIKA: Kilimanjaro, near Bismarck Hill, 3220 m., in evergreen mist forest, *P. J. Greenway 3816* (both forms); * Dabaga, *Dr. Geilinger 1947, 6.IX.32*; at Kew.

NYASALAND: Nyika Plateau, ramicole, 2340 m., *L. J. Brass 17215*, in N. Y. Bot Gard. Herb.

23. USNEA DEMINUTA Motyka, Webbia 8:389. 1952.

Type: Ethiopia, Alto Semièn, Beleghes, Reg. Sancaber, 3300 m., *Pichi-Sermolli 2907*.

Thallus flaccid, pendent, 10–15 cm. long in type (more than 30 cm. long in our material), drying buckthorn brown on main axes, to yellow ochre or clay color on smaller branches; base absent in our plants, main axes 0.5–0.6 (–1) mm. in diameter, tapering upward; terete, articulate, many of the larger joints impressed to foveolate or even perforate, epapillate, up to 10 mm. long, mostly shorter, constricted at the ends, cracks narrow but showing the medulla or axis, the slender branches usually continuous, only slightly articulate, irregularly dichotomous; ramuli rare on the larger joints, occasional on the more slender branches, perhaps only undeveloped branches from an unequal dichotomy, and rare spinules which break away leaving minute scars and probably serve as isidia; pseudocyphellae minute on the larger joints, also short longitudinal or oblique cracks in the cortex through which medullary hyphae protrude.

Tangled with *Mearns 1776* is a fertile terminal fragment which seems to be this species. The axis is orange cinnamon shading to light vinaceous cinnamon at the tips, and is regularly annularly cracked, exposing the white medulla; the joints cylindric, rarely very slightly inflated and faintly longitudinally rugose with rare pseudocyphellae; the smaller branches show more pseudocyphellae and longitudinal cracks. The apothecia are 2–4 mm. in diameter, cupulate, sessile; exciple smooth except for several very deep, rounded foveolae on either side of the concrescent branch; marginal cilia distant, of variable length, the shorter nearly erect, the longer spreading and curved, about 5 mm. long, annularly cracked at the base with a few very minute pseudocyphellae; disc very concave, white-pruinose.

Our specimens have been referred here although the dimensions are slightly larger and I have seen no material from Ethiopia. They have been found tangled with other much larger species of the section ARTICULATAE, but do not resemble the juvenile forms of those species.

KENYA: west slope of Mt. Kenya, trail from West Kenya Forest Station to summit, in bamboo zone, ca. 3000 m., *Edgar A. Mearns 1776* p. p. (T. Roosevelt Exp.), at Farlow Herb.

UGANDA: Imatong Mts., Mt. Kineti, 2810 m., ramulicole, *A. S. Thomas 1873*, at Kew.

TANGANYIKA: S. Pare Mts., Mtonto, 2100 m., on bushes of *Philippia, P. J. Greenway 6532a*, in E. African Herb.

24. USNEA ARTICULATA (L.) Hoffm. subsp. AETHIOPICA Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Ethiopia, below Debra Erki, on fir, *Schimper 18*, 21 Oct. 1850, det. *U. articulata* v. *intestiniformis* Ach. by Müller Argau.

Thallus pendent, more than 25 cm. long, probably flaccid (now glued tightly to herbarium sheet), snuff brown; base about 1 mm. in diameter, 8 mm. long, annulate, not blackened, then about twice closely dichotomous and occasionally so

throughout; articulate, joints irregular in size in the same axis, straight or curved and cucumiform, the larger joints mostly basal but not always so, 25–30 mm. long, 4–5 mm. in diameter (crushed flat in drying and hence appearing up to 7 mm.), the smaller joints 5–10 mm. long, about 1–1.4 mm. in diameter, usually straight, occasional branches long and slender, scarcely articulate and occasionally quite closely ramulose; ramuli slender, about 5 mm. long; the larger joints often foveate to scrobiculate, with small slightly elevated pseudocyphellae, sometimes in rows, the smaller joints smooth with minute pseudocyphellae; the smallest almost non-articulate branches with small soralia of isidiose soredia.

Superficially our pressed plant, glued tightly to the herbarium sheet, resembles subsp. *intestiniformis* (Ach.) Crombie, in habit and color. The latter grows on sandy soil in England, France, Belgium, and the Netherlands. The main axes are more uniform in diameter and larger with relatively shorter joints, pseudocyphellae quite rare, and no soralia have been observed. Our plant is apparently more closely related to subsp. *Kotschyana* Motyka from Syria, 40 cm. long, with joints smaller and more uniform in size, coarsely papillate and sorediose. I am unable to estimate the size of our plant as the upper portion of the main axes has been broken away; the portion present measures 25 cm. long.

ETHIOPIA: below Debra Erki, on fir, *Schimper 18*, 21 Oct. 1850, det. as *U. articulata* v. *intestiniformis* (Ach.) Crombie, at Kew.
KENYA: Gilgil, on trees, *G. M. Allen 1780*, in Howe herb. at Farlow Herb.

25. USNEA TERRESTRIS Motyka, Lich. Gen. Usnea Stud. Monog. 75. 1936.

Type: Tanganyika, Mt. Kilimanjaro, 4000 m., on rocks in grassland, above tree-line, *H. Meyer*.

Thallus prostrate or pendent, pale gray green when fresh, drying tawny olive on larger branches to warm buff on the capillaceous summits, up to 20 cm. long, base very dark brown, about 1–3 mm. in diameter and 1 mm. tall, fraying out below into many root-like fibers enclosing soil particles and expanding above to 2 mm. in diameter at the first fork; dichotomous, constricted at the axil, articulate, joints 7–20 mm. long, constricted at the ends, lower joints inflated to 2 mm. in the middle, the upper ones to 1 mm., separate or cortex continuous, tapering with closer ramuli and repeatedly dichotomous branching to the capillaceous summits, tips of ultimate branches acute, slightly blackened; surface smooth to impressed and subfoveate, becoming nearly terete at the summits; ramuli rare on the larger branches, perpendicular, straight or slightly curved, articulate at the base but not inflated, tips acute, longer, and more slender, abundant on the summits but never crowded, mostly 5 mm. or less long, a few much longer, subtuberculate and occasionally pseudocyphellate; pseudocyphellae white, very small and inconspicuous, round or elongate; soredia clearly seen only on James' specimen from Kenya, abundant on smaller branches, from rather large, farinose, pale sulfur soralia, hemispheric, rarely crateriform when eroded, very rarely substipitate.

The above description is based mostly on *Turrall 71* from the type locality, as the specimen agrees well with Motyka's description although a little larger and with inconspicuous pseudocyphellae, easily overlooked, and with soralia. *Burtt 4071* from Mt. Meru is a tangled mass of many plants with fragments of dead mosses glued to the herbarium sheet. The one plant I succeeded in disentangling appears smaller and younger, only 11 cm. long, but is morphologically similar. Burtt's specimen from Ruanda is a fragment, slightly darker, mostly terete, rarely impressed, with very rare pseudocyphellae. Apparently broken smaller branches and the ultimate branches are capable of forming a new holdfast and continuing to develop new secondary axes. Burtt's specimen seems to be a fragment of one of these secondary axes.

James' specimen from Kenya is a mass of plants glued to the herbarium sheet, evidently terrestrial, as the mass contained a small pleurocarpous moss, bits of dead leaves, and very rotten twigs, dead grasses and scraps of *Parmelia*. The plants are tawny olive to Sayal brown, the capillaceous summits cinnamon buff to chamois, the joints on some of the principal axes 20 mm. long, 6.5 mm. in diameter (up to 10 mm. when pressed flat), thus suggesting *U. articulata* subsp. *aethiopica* Dodge, but these large joints are shorter and foveate and occasionally with a small soralium, or a short farinose ridge; soralia abundant and well developed on the smaller branches.

KENYA: Aberdare Mts., *Sir Evan James*, 1905, at Kew; w. slope of Mt. Kenya, 4200 m., *Edgar A. Mearns 1654* (T. Roosevelt Exp), in Mo. Bot. Gard. Herb., det. Motyka, and at Farlow Herb.

TANGANYIKA: Kilimanjaro, Bismarck-Peters, 3420 m., *R. G. Turrall 71*, at Kew and E. African Herb.; ober Waldrand, 3000 m., *Dr. Geilinger*, at Kew; Arusha District, Mt. Meru, 4680 m., *B. D. Burtt 4071*; at Kew; all on volcanic rocks in alpine meadows above tree line.

CONGO: Ruanda, Mufumbiro Mts., Mt. Mikeno, among grasses, *B. D. Burtt*, at Kew.

26. USNEA RUGOSA Motyka, Lich. Gen. Usnea Stud. Monog. 113. 1936.

Type: Ethiopia, Bagla, 2700 m., *Hildebrandt*.

Thallus pendent, flaccid, up to 65 cm. long, olive buff on the main axes, pinkish cinnamon on slender branches in recent specimens (2 years old), finally light brownish olive to Isabella color on the main axes, lighter on slender branches in older specimens (22 years old); holdfast inconspicuous, base up to 15 mm. long, 0.6–1 mm. in diameter, infrequently dichotomous throughout; articulate, joints mostly 2 mm. in diameter on main axes with an occasional joint up to 4 mm., varying in length from 2 to 10 mm.; surface variable, some joints smooth, terete, others with inconspicuous pseudocyphellae and low, narrow, farinose, more or less longitudinal ridges, the larger joints somewhat compressed and foveate with dense patches of dichotomous ramuli which may grow out to form the long secondary, capillaceous branches, up to 15 cm. long, surface asperate with punctiform soralia, somewhat larger and isidiose soralia on some of the basal joints; pseudoramuli arising from unequal dichotomies in the slender portion of the thallus.

Only lateral apothecial initials seen in our material. Motyka describes the apothecia as lateral, about 5 mm. in diameter, exciple very thin, plane, smooth; marginal cilia small, variable in length, flexuous, articulate; disc nearly plane, rugose; thecium 60 μ tall; asci ventricose; ascospores 7 $\times$ 9 μ, with a thin epispore.

Hildebrand 307 at Kew seems to be this species; the color is uniformly clay color, mostly with a white pruina from excess of mercuric chloride in poisoning; the main axes are rather more slender and smoother, sterile. It may be a duplicate of the type or perhaps of the specimen cited by Motyka as *U. articulata* subsp. *mediterranea* Mot. which, however, remains pale stramineous or very pale olive fuscous in the herbarium. There is a discrepancy in the elevation cited for the type; in the citation before the description, Motyka gives 2700 m., while in the citation of specimens seen at the end he gives 2420 m. The specimen at Kew is given as 7500 ft. (2420 m.).

ETHIOPIA: Galla Pass, 9° 28′ N., 42° 19′ E., *J. B. Gillett 5130*, Abyssinia-Somaliland Bound. Comm.; Simien, Mindigabsa, *H. Scott 323*; Bagla, 2420 m., *J. M. Hildebrandt 307*; all at Kew.

27. USNEA VAINIOANA[1] Zahlbr., Cat. Lich. Univ. 6:597. 1930.

Usnea fragilis Vainio, Hedwigia 37:40. 1894, non Stirton. 1882.

Type: Uganda, Mt. Ruwenzori, 0° 5′ S., *Scott-Elliott*.

Thallus up to 30 cm. long, pendent, very flaccid, rather fragile when dry, between colonial buff and olive buff, one group of plants cream buff after drying; base 5 cm. long, 0.6 mm. in diameter, annularly cracked; holdfast conic, 1 mm. in diameter, black; main axes 0.6 mm. in diameter, tapering gradually at each dichotomy to long capillaceous summits; branching infrequently dichotomous, the larger branches articulate, joints up to 5 mm. long, not or very slightly inflated below, not constricted at the ends, terete or very slightly impressed to subfoveolate, smooth, eramulose (less-developed branches may simulate ramuli); summits capillaceous, flexuous. Apothecia and soredia not seen in certain material.

Turrall 55 in the E. African Herbarium and a fragmentary plant untangled from another species in specimens from Kew seem to be this species. The main axes are up to 1 mm. in diameter, the joints somewhat more inflated, some slightly more foveolate or very slightly rugose; medulla K—. Apothecia very rare, lateral on smaller branches, 0.3 mm. in diameter, exciple subimpressed, very slightly pruinose; disc plane, 2 mm. in diameter, pale carneous, densely white-pruinose with 6–8 marginal cilia of variable length. This plant seems to be intermediate between *U. Vainioana* Zahlbr. and *U. exasperata* (Müll. Arg.) Vainio.

ETHIOPIA: Simien, Mindigabsa, *H. Scott 323a*; Geech, *H. Scott 250*; both at Kew.

TANGANYIKA: Mt. Kilimanjaro, 2900–3030 m., on giant heather, *R. G. Turrall 55*, in E. Africa Herb., fragment at Kew; S. Pare Mts., Mtonto, 2100 m., *P. J. Greenway 6532*, in E. African Herb.

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., ramicole, *L. J. Brass 16846* (Vernay Nyasaland Exp.), in N. Y. Bot. Gard. Herb.

[1] Original spelling *Wainioana* corrected by Motyka (Lich. Gen. Usnea Stud. Monog. 437. 1937) to conform to Vainio's preference for spelling his name after the Finnish revolution.

28. USNEA GRACILIS Ach., Lichenogr. Univ. 627. 1810.

Type: Ile Réunion (Bourbon), com. *Weber & Mohr.*

Thallus pendent, up to 30 cm. long, flaccid, gray to pale green, becoming deep olive buff in the herbarium; the main branches often Natal brown or darker in the lower portion; base hemispheric, attached to the bark; immediately dichotomous and repeatedly so throughout, often unequally so when one branch resembles a long, slender curved ramulus; lower portion of the main axes about 0.7 mm. in diameter, gradually tapering to the capillaceous summits; terete, continuous or annulate with very minute cracks, smooth, with rather indistinct paler lines; soredia unknown.

Apothecia very rare, sessile on smaller branches, up to 4 mm. in diameter, cupulate to subplane; exciple smooth; marginal cilia distant, 2–10 mm. long, annularly cracked at the base, tapering to acute tips; disc flesh color, faintly white-pruinose.

Cortex 90 μ thick, fastigiate, highly gelified; algal layer about 40 μ thick, cells protococcoid, 6–7 μ in diameter, dying in the older portions of the thallus and leaving cavities; medulla 225 μ thick, of densely woven hyphae 3–4 μ in diameter, lumen 1 μ; axis 275 μ in diameter, of conglutinate, thick-walled longitudinal hyphae. As the duplicate of *A. G. Allan* from Kenya in Herb. Bouly de Lesdain is cited by Motyka, probably his statement "medulla tantum ca. 20 μ crassa" is a misprint for 200 μ.

ETHIOPIA: without locality, *J. Omer-Cooper*, at Kew.
KENYA: Ngongo Bagas, *A. G. Allan*, com. Rev. W. Lillie, in Howe herb. at Farlow Herb.
TANGANYIKA: E. Usambara, Amani-Maramba, 1030 m., *P. J. Greenway 4151.*
CONGO: Mt. Kahusi, ca. 2700 m., on *Arundinaria alpina, F. L. Hendrickx 4300, 4302, 4314*, sparingly fertile, in E. African Herb.
NYASALAND: Mt. Mlangi, 1450–2250 m., *P. J. Greenway 6332.*
MAURITIUS: without locality or collector, ex herb. Macreight in Tuckerman Herb., sub *U. plicata* at Farlow Herb.
RÉUNION: com. Müller Argau, at Farlow Herb.

29. USNEA PULCHELLA Motyka, Lich. Gen. Usnea Stud. Monog. 442. 1937.

Type: St. Helena, Diana Peak, *Dumont d'Urville*, at Uppsala, not seen.

Thallus pendent, very flaccid, 25 cm. long (45 cm. in our specimens), drying bister to snuff brown on the main axes, pinkish cinnamon to cinnamon buff on slender branches and ramuli; holdfast a small black disk under the outer layers of bark cells, the base growing outward through a crack, 10 mm. long, 1 mm. in diameter, curving downward, annularly cracked, the part within the bark black; repeatedly dichotomous throughout, internodes somewhat shorter near the base and in the capillaceous summits; larger branches articulate, joints of variable length and diameter, some slightly inflated, up to 1.3 mm. in diameter, mostly about 1 mm. in diameter, others on the same branch shorter, cylindric, about 0.8 mm. in diameter, smooth, or on the slenderer, less articulate branches, very minutely white tuberculate (or pseudocyphellate?); the larger branches almost

eramulose, the slender branches quite irregularly ramulose; ramuli 10–40 mm. long, the shorter slender, straight or curved and smooth, the longer somewhat tuberculate and occasionally once or twice dichotomous (perhaps arrested development of a branch), usually flexuous; sometimes several growing out at a "node" forming a tuft (as in *U. nidifica*) in the type, absent in our specimens.

It seems quite likely that *U. monumenti* Fée,[1] type from St. Helena, trees about Napoleon's tomb, without collector, is the same species, but I hesitate to reduce *U. pulchella* Motyka to synonymy without seeing the types. *U. Lyngei* Motyka, from the same locality as *U. monumenti* Fée, has minute white farinose tubercles and ramuli not in dense clusters. *U. umbrata* Motyka, also from St. Helena, is very rigid and less articulate.

Our plants are longer and somewhat more slender than the type (*fide* Motyka) and have minute white tubercles which probably develop a few isidiose soredia. Perhaps the tufts of ramuli mentioned by Motyka are such isidiose soredia which have developed *in situ*. Otherwise our plants agree well with Motyka's description.

FERNANDO PO: Santa Isabel Peak, 2900 m., *Gustavo Mann 682*, probably arboricole, 2 sheets at Kew.

30. USNEA MONILIFORMIS Motyka, Lich. Gen. Usnea Stud. Monog. 447. 1937.

Type: S. Africa, Natal, hills above Mauritzburg, *Anton Rehmann*.

Thallus pendent, up to 30 cm. long, flaccid, lower portions of main branches sepia shading upward to cream buff at the summits, somewhat shining; holdfast a disc 2 mm. in diameter, base blackened, about 2 mm. long, 0.5–0.7 mm. in diameter; several times dichotomous near the base, some of the secondary branches forming holdfasts, then less closely dichotomous throughout; eramulose (occasionally one branch develops more slowly and resembles a ramulus); main branches 0.5–0.7 (–1) mm. in diameter, thinning at each dichotomy, summits capillaceous; terete, closely annulate, joints 1–3 (–10) mm. long, not constricted at the ends, cracks narrow, white-margined; very smooth, variegated with white points and lines (pseudocyphellae ?), very rarely the lines are slightly elevated.

Superficially, this species somewhat resembles *U. gracilis* with somewhat the same geographic distribution at low elevations, but with a thicker, laxer medulla and darker fuscous color. If the white points and lines are considered as pseudocyphellae, it would suggest inclusion in the ARTICULATAE instead of the STRAMINEAE-AMOENAE and a relationship to *U. deminuta* Motyka from Ethiopia at much higher elevations.

KENYA: Ngong hills, 2370 m., *P. R. O. Bally B94;* Marsabit Mt., *A. T. A. Ritchie*, com. *P. R. O. Bally B1416*; at Kew.

TANGANYIKA: Kilimanjaro, near Bismarck Hill, 3220 m., in evergreen mist forest, *P. J. Greenway 3816;* Marangu, Bismarck, 2140 m., *R. G. Turrall 37*, at Kew.

CONGO: Mt. Kahusi, 2700 m., on Ericaceae, *F. L. Hendrickx 3440*, in E. African Herb.

[1] In Dictionnaire Classique (ed. Bory de St. Vincent) 16:481. 1830.

31. USNEA STRAMINEA Müll. Arg. emend. Motyka, Lich. Gen. Usnea Stud. Monog. 466. 1937; Müll. Arg., Flora 62:162. 1879, p. p. excl. syn.

Type: Mauritius, *Robillard* at Genève, a portion in Farlow Herb., selected by Motyka as type. The New Zealand specimen from Nelson, com. Ferd. v. Müller, also cited by Müller Argau, is referred by Motyka to his var. *substraminea* as well as the types of the synonyms cited by Motyka.

Thallus pendent, more than 20 cm. long, somewhat flaccid, pale stramineous when fresh, main axes drying hazel or lighter, ramuli warm buff, shining; holdfast and base broken off in material available; several times closely but somewhat unequally dichotomous near the base, then rarely so above, axils about 90° angles, the branches curving downward, nearly parallel, about 1 mm. in diameter, somewhat flexuous, annularly cracked and subarticulate, terete, some joints not constricted at the ends, some with surface slightly foveate, and some sparsely low-tuberculate (probably initials of ramuli); secondary branches 0.3–0.5 mm. in diameter, about 10 cm. long, foveolate, cortex more or less longitudinally cracked, forming elongate soralia, shorter and nearly circular above, soredia granular; ramuli 10–20 (–30) mm. long, very slender, infundibuliform at the base, annularly cracked just above, low-tuberculate and small-soraliate, tapering to an acute tip; summits capillaceous, distantly short-ramulose.

Cortex very fragile when dry, 115 μ thick, fastigiate, highly gelified; algal layer 65 μ thick, of discrete flattened colonies of *Trebouxia* 20–25 μ in diameter, separated by strands of closely woven medullary hyphae; medulla 300–350 μ thick, the outer 100 μ very compact, of predominantly periclinal hyphae, the inner portion of very loosely woven radial hyphae, occasionally dichotomous, 4–5 μ in diameter, very thick-walled, heavily nubilated with minute hyaline granules, arising as branches of dark brown periclinal hyphae, 6–7 μ in diameter; axis 360–400 μ in diameter, hyaline, of thick-walled longitudinal conglutinate hyphae.

The Socotra plant, referred here by Müller Argau, has a main axis about 2 mm. in diameter, is more clearly articulate with joints somewhat constricted at the ends and deeply foveate.

MAURITIUS: *Robillard*, portion of type com. Müller Argau, at Farlow Herb.
SOCOTRA ISLAND: *Schweinfurth*, com. Müller Argau, at Farlow Herb.

32. USNEA EXASPERATA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 440. 1937.

Usnea dasypogoides v. *exasperata* Müll. Arg., Flora 73:336. 1890.
Usnea dasypoga v. *exasperata* Zahlbr., Cat. Lich. Univ. 6:556. 1930.

Type: Tanganyika, Kilimanjaro, 3000 m. [3145 m., *fide* Stein in Meyer, Across E. African Glaciers, 353. 1891], *H. Meyer* in Genève; portion of same collection in Berlin, typical; another in Breslau, up to 60 cm. long, branches papillose and verruculose, probably an unnamed species.

Thallus 30–35 cm. long, pendent, flaccid, pale yellow when fresh, fawn to wood brown below, shading to vinaceous buff above, the ramuli and long capillaceous summits colonial buff to olive buff; holdfast a black verrucose disc giving rise to several axes, base 3–4 (–10) mm. long, about 0.8 mm. in diameter below, increasing to about 1.2 mm. in diameter just below the first branch, the lower third black, annulate; closely and somewhat unequally dichotomous in the lower 4 cm., with very short internodes, then very rarely dichotomous in the next 10–12 cm., about 1 mm. in diameter, tapering upward, then once or twice dichotomous at the bases of the very long, capillaceous summits; the larger branches subfoveolate, closely articulate, joints not or only very slightly inflated, axils somewhat complanate, very rarely ramulose; the upper portions of the main branches slightly obliquely rugose, the joints longer and the axils not complanate, the cortex sometimes subareolately cracked, the cracks white-margined, not verrucose nor papillate; ramuli 10–30 mm. long on the larger branches, perpendicular to the axis but variously curved and twisted, only 4–5 mm. long on the slender capillaceous portion of the thallus, with small low tubercules which probably develop minute isidiose soredia on most of the ramuli, although only a few have developed so far in our plants. Medulla K— or slowly yellow.

Apothecia (in *Hendrickx 4330*) 2–3 mm. in diameter, lateral on slender branches or large ramuli; exciple nearly plane, smooth or nearly so; marginal cilia subdistant, up to 10 mm. long, curved, annularly cracked at the base and sparingly so above, slender; disc carneous, white-pruinose.

Turrall 37 is sterile and quite sorediose, but apparently belongs here. The material from Kikuyu, Kenya, is only a fragment, the joints somewhat longer and more inflated, the tubercles on the smaller branches forming slightly elevated isidiose soralia. Some of the broken branches have regenerated dense clusters of short ramuli, about 3 mm. long.

KENYA: Kikuyu, *without collector, no. 39*; Elgon, *Miss R. J. Bush*, in E. Africa Herb. 10,573; Aberdares, *W. J. Dowson 293*, at Kew.

TANGANYIKA: Kilimanjaro, Marangu-Bismarck, 2140 m., *R. G. Turrall 37*; Bismarck Hill, 3220 m., *P. J. Greenway 3816*, at Kew.

CONGO: route Kahusi, 2450 m., on *Hagenia*, *F. L. Hendrickx 3679*; Mt. Kahusi, ca. 2700 m., *F. L. Hendrickx 4300, 4305, 4308, 4311, 4316, 4330*; all in E. African Herb.

33. Usnea Pinkertonii Stirton, Scottish Nat. 6:294. 1882.

Type: Egypt, Petrified Forest near Grand Cairo, *Pinkerton*, in the Art Galleries of the Glasgow Corporation.

Thallus 18 cm. long in type, over 25 cm. in our plants, pendent, flaccid, buffy brown on main axes to citrine drab on smaller branches; base blackened and rather hard in type, absent in our specimens, infrequently dichotomously or sympodially branched on the main axes, more closely so on the smaller branches; main axes up to 1 mm. in diameter, closely articulate, joints very slightly inflated, slightly rugulose and subfoveolate, some very minutely and acutely papillate especially in the

mid-portion of the thallus, others epapillate, backs of ridges often white-punctate (pseudocyphellae ?); ramuli irregularly disposed, sometimes quite close, sometimes absent for some distance on the main axes and secondary branches, usually close on the smaller branches, very slender, mostly 2–3 mm. long, some up to 7 mm.; summits capillaceous, very densely branched.

Apothecia lateral on secondary branches, up to 10 mm. in diameter, cupulate becoming nearly plane; exciple smooth in smaller apothecia, slightly rugulose and subpapillate on the larger ones; marginal cilia quite close, rather long, the longer often forked; disc dark carneous, white-pruinose at first, becoming nearly nude in age.

Although placed by Motyka in the BARBATAE, subsect. PENDULINAE, the olive fuscous color, the very thin cortex and thick lax medulla, the subarticulate thallus with rugose to subfoveolate joints all point to a close relationship to the STRAMINEAE subsect. SULCATAE, although papillae are very rare in the STRAMINEAE except in *U. straminea* Müll. Arg. *Bally 5611* seems to belong here. The specimen consists of the upper portion of a main axis and six secondary branches. No papillate joints were seen.

EGYPT: Petrified Forest near Grand Cairo, *Pinkerton*, in Art Galleries of the Glasgow Corporation.

ETHIOPIA: Galla Pass, 9° 28′ N., 42° 19′ E., 2520 m., *J. B. Gillett 5130*, Abyssinia-Somaliland Bound. Comm.; Simien, Mindigabsa, *H. Scott 323b*, sterile; both at Kew.

KENYA: Northern Frontier Province, 1560–1610 m., on *Cineraria grandiflora*, *P. R. O. Bally 5611*, at Kew.

34. USNEA CAMEROONENSIS Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Cameroons, *Miss Cheeseman L3*, at Kew.

Thallus pendent, rather flaccid, more than 55 cm. long, main axes drying snuff brown, Sayal brown to cinnamon, ramuli deep olive buff, base broken away; articulate, joints about 1.5 mm. in diameter below, mostly 1 mm. above, thinning gradually; closely several times dichotomous below, then unbranched for 10–20 cm., occasionally dichotomous above; axils subcomplanate, joints variable in length, many about 10 mm. long, constricted at the ends, usually showing the axis in the cracks, not or only very slightly inflated, longitudinally rugose, the ridges low, cracked at the top and farinose, flattened but not sulcate between; ramuli irregularly disposed throughout, up to 30 mm. long on the main axes, base subarticulate and inflated, tapering to a slender acute tip, about 10 mm. long on the secondary branches, surface low-tuberculate and deformed, forming isidiose soredia which soon break away causing the tops of the tubercles to appear farinose, somewhat in rows in the lower portions. Apothecia not seen.

Cortex 55 μ thick, fastigiate in a gel, outer 8–10 μ nubilated with minute brownish crystals; algal layer 30 (–40) μ thick, of densely packed protococcoid cells 6–8 μ in diameter; medulla 185–195 μ thick, of loosely woven thick-walled hyphae 3 μ in diameter, somewhat more compact next the algal layer; axis 250 μ

in diameter, of conglutinate, thick-walled hyphae 5–6 μ in diameter, lumen 3 μ and in the central portion a few large brownish hyphae 6–8 μ in diameter, nubilated with minute brownish crystals.

CAMEROONS: *Miss Cheeseman L3*, at Kew.

35. USNEA FUSCA Motyka, Lich. Gen. Usnea Stud. Monog. 473. 1937.

Type: S. Africa, Transvaal, Lydenburg, *Wilms*.

Thallus pendent, up to 20 cm. long (30 cm. in our material), green becoming buffy brown on the main axes, shading to honey yellow or chamois on the smaller branches; holdfast thin, circular, 2–3 mm. in diameter, darker but not black, base 1–2 mm. long, about 0.5 mm. in diameter, then dichotomous at right angles and the branches pendent from opposite sides of the branch of the tree, rarely dichotomous in the next 4–10 cm., then more frequently and more closely so near the summits, flexuous to nearly straight; main axes up to 1.5 mm. in diameter, articulate, joints variable in length, cylindric or very slightly inflated, not or only slightly constricted at the ends, nearly terete but somewhat deformed to obtusely angled, rugulose, the ridges oblong and mostly oblique, backs ecorticate and farinose, cortex sometimes cracked and subareolate; axils of larger branches flattened; ramuli almost absent below, more frequent above but perhaps only members of unequal dichotomies; summits long-capillaceous. Apothecia not seen. Soredia isidiose, becoming farinose from tubercles of the main axes, very small-punctate, not elevated on the smaller branches.

In the northern portion of its range, whence our material came, the species assumes more the habit of *U. exasperata*; cf. specimen from Kilimanjaro, *Uhlig*, cited by Motyka, loc. cit. 474.

KENYA: Chyulu Hills, *H. D. van Someren* (2 sheets in E. African Herb.).
UGANDA: Kigezi, Mafuga, 2580 m., *I. R. Dale L41*, fragments; Toro, Fort Portal, 1625 m., *I. R. Dale L40*, fragments tangled with other spp.; both at Kew.
TANGANYIKA: S. Pare Mts., Mt. Mtonto, 2100 m., *P. J. Greenway 6532*, at Kew.
CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4314* (native name: *ndendu mushi*), in E. African Herb.

36. USNEA DECIPIENS Motyka, Lich. Gen. Usnea Stud. Monog. 477. 1937.

Type: Tanganyika, Mt. Msimbwa near Lake Tanganyika, 2300 m., corticole, *Münzner*.

Thallus pendent, somewhat rigid, over 40 cm. long, sepiaceous-fuscous (snuff brown on larger branches, Isabella color on small branches in our material), smooth, almost shining; base indistinct, 3 mm. long, 1 mm. in diameter, expanding to 2 mm. at first branch, not blackened in our material; main branches 2 mm. in diameter below, tapering very slowly, rarely and irregularly articulate, only slightly constricted, fractures indistinct, acutely angled or subterete with distinct longitudinal (rarely somewhat oblique) ridges, backs pale, very deeply foveate or impressed, with very rare pseudocyphellae between; ramuli close, large and small

intermingled, the smaller 5 mm. long, the larger almost as large as the branches, thick at the base, tapering above to obtuse tips, continuous or rarely slightly articulate, often arcuate and contorted ridges, closer and less regular; summits indistinct, of longer and denser ramuli.

Our Uganda material is rather fragmentary, tangled with *U. vesiculata*, both species glued to the herbarium sheet. The above description is taken in part from Motyka's monograph. Our material differs in having the main axes almost eramulose, the ramuli irregular on the secondary branches, sometimes quite close, in others rather scattered. Some of the ramuli have tubercles developing hemispheric isidiose soralia which appear farinose after the isidia are shed.

UGANDA: Elgon, Madangi, 3550 m., on heath trees in alpine meadow, *A. S. Thomas 607 p. p.*, at Kew.
KENYA: Mt. Kenya, Kinangop, Aberdare, 2840–2900 m., on trees, *P. Chandler 2278*, ex hb. Botanist Dept. Agr. Uganda, at Kew.

36a. Var. RHODESIANA Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Southern Rhodesia, Matopos District, top of high granite hill, 1610 m., on tree, *Frederick Eyles 1023*, at Kew.

Thallus pendent, subflaccid, over 30 cm. long (incomplete), Isabella color, ramuli somewhat lighter; base not seen; infrequently dichotomous, not articulate nor annulate, longitudinally and subreticulately rugose, ridges subacute, cortex often cracking along the ridges, subareolate and somewhat scaling, deeply foveolate or sulcate between the 6–10 ridges per circumference of transverse section, about 1 mm. in diameter, thinning to about 0.5 mm. in the upper 15 cm., but summits not capillaceous; ramuli close throughout, 3–15 mm. long, the longer perhaps arrested branches as they are sparsely and minutely ramulose or bear low tuberculiform, farinose soredia.

Cortex 40 μ thick, fastigiate, pseudoparenchyma cells 5–6 μ in diameter, nubilated with brownish crystals in the outer 15 μ; algal layer 30 μ thick, nearly continuous except in cortical cracks, cells protococcoid; medulla 30–40 μ thick, of densely woven mostly periclinal slender hyphae; axis 600–625 μ in diameter, slightly angled, of uniformly longitudinal, conglutinate thick-walled hyphae.

The cortex and medulla are proportionally much thinner than in *U. decipiens* and the ramuli closer and more sorediose.

37. USNEA AEQUATORIANA Motyka, Lich. Gen. Usnea Stud. Monog. 476. 1937.

Type: Uganda, Mt. Ruwenzori, 2900–3220 m., *Scott-Elliott*.

Thallus pendent, up to 60 cm. long, flaccid, main axes bister to snuff brown, ramuli and capillaceous summits buffy olive or lighter; holdfast black, about 3 mm. in diameter, an interwoven mass of root-like fibers penetrating the bark; base articulate, about 0.8 mm. in diameter below, rapidly expanding to 1 mm. or more, about 2 mm. long, then several times dichotomous forming several main axes, then very rarely dichotomous, about 1 mm. in diameter, slowly tapering to the long

capillaceous summits; articulate, joints not or very slightly inflated, slightly constricted at the ends in the larger branches, cylindric in the smaller branches; larger branches slightly but distinctly angled, ridges longitudinal, few, backs white-pruinose, rarely only slightly sulcate or foveolate, smaller branches smooth, terete, mostly ramulose; ramuli 4–5 mm. long, curved, bases thick, tips acute, rather dense but with sections of the principal axes almost eramulose. Soredia not seen.

Apothecia common, up to 10 mm. in diameter, mostly smaller, subterminal on lateral branches, exciple smooth except for 3–5 low, rounded, radiating ridges, a few of the larger apothecia subfoveate or impressed; marginal cilia dense, up to 10 mm. long, patent or recurved, thick, annulate; disc subconcave to almost plane or somewhat deformed, white-pruinose.

ETHIOPIA: without locality, *Schimper*, ex Herb. Sbarbaro sub *U. florida* v. *strigosa*, at Farlow Herb.

KENYA: Endabarrá, Mau forest, 2350 m., in *Acacia* grove at forest edge, *P. R. O. Bally B4947*; uplands, 2250 m., *E. R. V.*, ex Corydon Mus. Kenya 5161, at Kew; Mt. Elgon, 2790 m., *E. J. Lugard & Mrs. Cyril Lugard 490*, at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., *I. R. Dale L. 43*; Imatong Mts., Mt. Kineti, *A. S. Thomas 1893*, both at Kew.

38. USNEA FLACCIDA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 475. 1937.

Usnea angulata v. *flaccida* Müll. Arg., Flora 73:337. 1890.

Type: Kenya, Leikipia at foot of Aberdare Mts., corticole, *L. von Hoehnel 176*.

Thallus pendent, flaccid, ca. 13 cm. long (Motyka), up to 30 cm. long in our material, becoming buffy brown on main axes, ramuli somewhat lighter; base about 1 cm. long, 0.5 mm. in diameter; articulate, joints cylindric, with short ramuli, not blackened; then closely dichotomous, axils flattened, then less frequently dichotomous throughout; flexuous, articulate, joints not inflated, up to 1 mm. in diameter below, thinning at each dichotomy but mostly about 0.5 mm. with long capillaceous summits; few elevated, acute ridges on the lower foveate joints, less ridged above, the upper joints almost cylindric, otherwise smooth; ramuli rather close, evenly distributed throughout, slender, 0.3–10 mm. long, somewhat curved.

Apothecia absent in the type and in our material. Motyka reports a specimen from Kilimanjaro, 3300 m., *Uhlig*, with apothecia up to 10 mm. in diameter, sublateral, thin, exciple plane or slightly concave, distinctly foveolate; marginal cilia few, slender, variable in length, flaccid; disc plane or slighly convex, often tuberculate-deformed; thecium 50 μ tall; ascospores 7 $\times$ 10 μ, ellipsoid, in narrow asci.

SUDAN: Imatong Mts., Mt. Kippia, pendent from twigs of trees in grassland, 2580 m., *A. S. Thomas 1823A*.

KENYA: Leikipia plateau and Aberdare Range, district around Nyeri, hanging from twigs, *W. Scoresby Routledge*, at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., on tree, *I. R. Dale L43*.

SOUTH AFRICA: Adelaide, *Miss D. K. Kingon*, com. Rev. W. Lilliè, in Howe Herb. sub *U. florida* v. *perplexans* (Stirton) Zahlbr. det. M. Bouly de Lesdain, at Farlow Herb.

39. USNEA TERRICOLA Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Cameroons, Mamoquilles, 2450 m., terricole among mosses and *Stereocaulon* sp., *Miss Cheeseman 25*, at Kew.

Thallus fruticose, subrigid, 8–10 cm. tall, cinnamon buff to buffy brown, irregularly black-maculate on the main axes, summits dark olive buff; base black, densely dichotomous at soil level, probably sending coarse root-like structures into the soil (broken off in collecting), rapidly expanding from 1 mm. to 2–3 mm. in diameter in the lower and middle joints, then tapering to 0.5 mm. in the ultimate joints; articulate, joints 5–20 (–30) mm. long, constricted at the ends, cracks varying from very narrow to 1 mm. wide, dichotomous throughout; basal joints nearly smooth with punctiform pseudocyphellae, and cortex cracked, forming low short ridges, sulfur-farinose, which may develop minute isidiose soredia; intermediate and upper joints more or less minutely verrucose with more abundant and elevated ridges, sometimes becoming reticulate and giving a foveate appearance, on the upper joint occasionally developing an apotheciform soralium covered with minute isidiose soredia, or part of the verrucae may form small elevated soralia. The soredia sometimes develop *in situ* producing dense clusters of pseudoramuli or becoming minute dichotomous thalli, joints only 0.3–0.5 (–1) mm. in diameter; summits obtuse.

Cortex 50 μ thick, loosely fastigiate in a gel, outer 20 μ nubilated with minute brown crystals; algal layer 35 μ thick, a continuous layer of densely packed protococcoid cells 8 μ in diameter; medulla 375 μ or more thick, of thick-walled hyphae 5–6 μ in diameter, very densely woven in the 50 μ next the algal layer, rest very lax, of predominantly radial hyphae; axis 300 μ in diameter, of conglutinate, longitudinal thick-walled hyphae, 3–4 μ in diameter.

CAMEROONS: Mamoquilles, 2450 m., terricole, *Miss Cheeseman 25*, at Kew.

40. USNEA HISPIDULA Motyka, Lich. Gen. Usnea Stud. Monogr. 488. 1937.
Usnea barbata v. *hispidula* Müll. Arg., Bot Jahrb. [Engler] 20:245. 1894.

Type: Tanganyika, Usambara, *Holst.*

Thallus about 15 cm. long, subpendent, quite rigid, fuscidulous in the herbarium, larger branches ochraceous tawny, ramuli dark olive buff, smooth; base absent in type, of rooting fibers penetrating bark at least 2 mm., not expanded into a holdfast, not blackened; primary branches 1.5–1.8 mm. in diameter, secondary branches thinner, constricted at the base, then slightly inflated and tapering gradually to the tips, continuous, or annularly cracked where the secondary branches leave the primary, smooth, with cylindric papillae (probably arrested ramuli); ramuli slender, 1–2 (–4) mm. long, minutely tuberculate and soraliate, forming all gradations between spinules and small tertiary branches; summits capillaceous, about 1 cm. long, tips acute, smooth or nearly so; soralia small, isidiose at first

becoming farinose, abundant on the smaller branches and the longer ramuli, rather rare on the larger branches.

UGANDA: Bugishu, Butandiga, 2130 m., arboricole, *A. S. Thomas 2565*, at Kew.
N. RHODESIA: East Isoka District, uplands, 1480 m., arboricole, *C. G. Trapnell*, a fragment lacking both base and summits, at Kew.

41. USNEA USAMBARENSIS Motyka, Lich. Gen. Usnea Stud. Monog. 489. 1937.

Type: Tanganyika, Usambara, Nguelo, *Kummer*.

Thallus up to 15 cm. long, pendent but quite rigid for its size, pale green when fresh, drying between deep olive buff and colonial buff; holdfast convex, about 2 mm. in diameter, not blackened; closely branched just above the holdfast, then less frequently dichotomous, branches nearly perpendicular, internodes variable in length, flexuous, about 1 mm. in diameter below to about 0.5 mm. above, summits mostly broken off, the few remaining about 2 cm. long, flexuous, tips obtuse, rather rigid, about 0.2 mm. in diameter; primary axis smooth, irregularly annulate and areolate, the areoles with raised margins; the middle portion rugose and low-angled, resembling *U. africana*; the upper portion, especially the smaller branches, low-tuberculate and deformed, the tubercles bearing a few rather coarse isidioid soredia, appearing farinose as the isidia break away, sometimes almost ecorticate in patches; ramuli subdistant, 2–3 mm. long, some longer, dichotomous, and resembling small lateral branches, flexuous, tapering from base to rather blunt tip, the shorter smooth, the larger minutely annulate and tuberculose, forming small soralia and eventually appearing decorticate.

Our plants from the Sudan are small, only about 5 cm. tall and only beginning to form soredia, probably juvenile. The plants from Madagascar are also small but quite punctate-sorediose above.

SUDAN: Onyiro, Issore, 1710 m., 32° 50′ E., 3° 50′ N., *T. F. Chipp 57*, at Kew.
MADAGASCAR: Imerina, Andrangoloaka, *Hildebrandt*, ex Herb. Sbarbaro sub *U. dasypogoides* v. *sorediosula* Müll. Arg., at Farlow Herb.

42. USNEA CARTILAGINEA Laurer in Motyka, Lich. Gen. Usnea Stud. Monog. 493. 1937.

Type: Cape of Good Hope, Table Mt., *J. F. Drège*.

Thallus 7–10 cm long, subpendent, quite flaccid, pale green, drying fuscous (Sayal brown to cinnamon), slender branches lighter; basal disc 2 mm. in diameter, base 1 mm. in diameter below, expanding rapidly to 2 mm. at the first branch, branching sympodial; branches articulate, joints inflated in the middle and constricted at the ends, not tapering upward, terete, smooth, with scattered minute tubercles below, closer above where they produce single small isidia; ramuli irregularly disposed and rare on the lower joints, more regularly subdistant above, straight, articulate, constricted at the base, inflated then tapering to a slender acute tip, indistinctly tuberculate, paler than the axes; summits more slender, less

conspicuously articulate, tips obtuse, more closely tuberculate, each tubercle producing an isidium, very rarely more. When the isidia are shed the remaining scars resemble minute white pseudocyphellae.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4316*; km. 30, route Kahusi, *F. L. Hendrickx 4322*; both in E. African Herb.

UGANDA: Mt. Elgon, 1290 m., arboricole, *W. Small 218*, at Kew.

SOUTH AFRICA: without locality, *Drège*, ex herb. W. Sonder, in Tuckerman herb. sub *U. florida*, at Farlow Herb.

43. USNEA TRANSVAALENSIS Vainio, Ann. Univ. Fenn. Aboens. A2[3]:1. 1928.

Usnea pectinata Stirton, Scottish Nat. 7:77. 1883, non Taylor.

Usnea tropica Zahlbr., Cat. Lich. Univ. 6:596. 1930.

Usnea florida v. *densirostra* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 1888/89: 145. 1890, excl. syn.

Type: Transvaal, Barbeton, saxicole, *P. A. van der Bijl 229*. The type of *U. pectinata* Stirton and *U. tropica* Zahlbr. is from S. Africa, Somerset East, *P. MacOwan*, in the Art Galleries of the Glasgow Corporation.

Thallus erect, fruticose, rigid, 3.5–5 cm. tall, pale green, becoming old gold to Isabella color; holdfast up to 4 mm. in diameter, of black, branched and tangled rootlets, formed by a coalescence of several plants or branching at the very base; primary axes 1–1.5 mm. in diameter, 2–6 mm. long to the first branch, not blackened, then closely dichotomous, almost at right angles, the branches curving upward; branches rare in the upper half, slightly constricted and annularly cracked at the base, about 0.8 mm. in diameter below, tapering upward to blunt tips; sparingly annularly cracked throughout, terete, glabrous below, appearing minutely verrucose above from the initials of soralia; ramuli very dense, mostly about 1 mm. long, a few up to 2 mm., tips blunt, very minutely verrucose but mostly covered with minute soralia of isidiose soredia which often germinate *in situ*, forming small isidia 0.1–0.2 mm. long, with blackened tips, and thus appearing secondarily ramulose; apothecia not seen.

Cortex 80 μ thick, fastigiate, highly gelified, the outer 10 μ with minute brownish crystals; algal layer 30 (–40) μ thick, continuous, cells protococcoid, 11–12 μ in diameter, somewhat polyhedral from mutual pressure; medulla 270 μ thick, of very loosely woven hyphae 3–4 μ in diameter, lumen about 1 μ, somewhat nubilated with hyaline granules; axis solid, 150 μ in diameter, of slender thick-walled, predominantly longitudinal hyphae.

The relationship of this species to *U. pulvinata* Fr., collected by Preiss in Western Australia, is not clear. Motyka's description is based on the whole complex from South Africa northward to Kenya. He states that the medulla is evanescently K yellow, while in the type of *U. transvaalensis* and in our material, the medulla is K yellow becoming red and finally reddish fuscous. He states that the ramuli are intermixed, short and long, up to 10 mm., not cracked at the base, and tips

subulate, often blackened; while in our material the ramuli are nearly uniformly 1 mm. long, with very few reaching 2 mm. In our plants the cortex is thicker and the algal layer and medulla are twice the thickness of the axis, while in *U. pulvinata* (*fide* Motyka) the cortex is thinner and the medulla only three fourths as thick as the axis.

UGANDA: Karamoja, Napak, 2250 m., on rocks in mountain grassland, *A. S. Thomas 3631*; Imatong Mts. 2100 m., *A. S. Thomas 1678*, both at Kew.
SOUTH AFRICA: Somerset East, *P. MacOwan*, type of *U. pectinata* Stirton non Tayl. and *U. tropica* Zahlbr., in the Art Galleries of the Glasgow Corporation.
MADAGASCAR: Imerina, Andrangoloaka, saxicole, *Hildebrandt 2172*; Prov. Betafo, *native collector*, ex Herb. E. G. Paris; both at Farlow Herb.

44. USNEA RUWENZORIANA Motyka in Zahlbr. & Hauman, Mém. Inst. Roy. Colon. Belg. 5:27. 1936.

Type: Congo, Mt. Ruwenzori, 4000 m., ramicole, *L. Hauman 929, 947*.

Thallus erect, 4 cm. tall, cespitose, pale ashy green, drying dirty fuscous (Saccardo's umber to light brownish olive in our plants); base hemispheric, 1.5 mm. in diameter, narrowing to 0.3–0.6 mm., 1–3 mm. to the first dichotomy, lower portion blackened; closely several times dichotomous near the base, axils 45–90°, main branches 1–1.2 mm. in diameter below, tapering gradually to short abrupt summits, terete, smooth, dull, rarely somewhat foveolate; ramuli quite dense, mostly about 2 mm. long, quite slender, slightly constricted at the base and somewhat inflated in the middle, some growing out as secondary branches; tubercles on summits and upper ramuli forming soralia, isidiose at first, soon eroded and farinose.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., arboricole, *I. R. Dale L43*; Bugishu, Butandiga, 2410 m., *A. S. Thomas 484* (slightly lighter in color, younger?); both at Kew.
TANGANYIKA: Kilimanjaro, 2900–2916 m., *R. G. Turrall 55*, at Kew.
CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4300*, in E. African Herb.

45. USNEA HAUMANII Motyka in Zahlbr. & Hauman, Mém. Inst. Roy. Colon. Belge 5:25. 1936.

Type: Congo, Mt. Ruwenzori, southwest slope, 4200 m., on *Senecio Friesorum* and *Helichrysum Stuhlmannii*, *L. Hauman 921*.

Thallus pendent, flaccid, up to 10 cm. long, pale ashy green, (larger branches tawny olive in our much older material), constricted at the base, then expanding rapidly to 1.5 (–2) mm. in diameter, irregularly dichotomous throughout, axils varying from 45 to 90°, irregularly curved, branches somewhat constricted at the base, rather thick throughout, irregularly annularly cracked, nearly terete, surface smooth or slightly rough from low tubercles (initials of small soralia?); ramuli very rare or absent, the few present suggesting that they are young branches arising from unequal dichotomy; summits indistinct.

Apothecia not seen. Soralia abundant on the slenderer branches, up to 0.2 mm. in diameter, sometimes crowded but rarely confluent, much smaller and more

scattered on the larger branches, subhemispheric, probably isidiose at first but mostly appearing farinose, some isidia germinating *in situ* and forming nest of propagula which early break away.

Our material from Cameroons consists of somewhat smaller plants, base broken away in collecting, color of the main branches darker (as they have been 23 years in the herbarium instead of 4 years at the time Motyka studied the type). Our plants were growing on stones, as were those from Kilimanjaro, 3500–4000 m., *Fr. & R. Wettstein*, cited by Motyka in his original description. The Uganda material is more typical. The Angola material is just beginning to form apothecia, sessile on the main axes for some distance back of the ultimate branches.

CAMEROONS: Mt. Cameroon, 4030 m., on bare rocky ground, *F. W. H. Migeod 196*, at Kew.

UGANDA: Kigezi, Muhavura, 3610 m., saxicole, *I. R. Dale L18*, at Kew.

ANGOLA: Cuanza Sul, Amboim, Capir near the Carloaongo-Cuvo River, 1000 m., on dead trees, *J. Gossweiler 9991a*, at Kew.

46. USNEA SIMPLICISSIMA Motyka in Zahlbr. & Hauman, Mém. Inst. Roy. Colon. Belge 5:29. 1936.

Type: Congo, Mt. Ruwenzori, 4000 m., on *Hypericum*, *L. Hauman 952*.

Thallus 5 cm. or less tall, simple or sparingly branched, subfruticose, pale green when fresh, drying between buckthorn brown and Dresden brown, opaque; base gradually but distinctly attenuate and blackened, several plants from a common holdfast giving a branched appearance; branches usually simple, somewhat curved, thickened to 1.3 mm. in diameter, subinflated, tapering from the middle upward, continuous or rarely articulate, constricted in the cracks, terete to slightly compressed and deformed, quite closely ramulose; ramuli 5–15 mm. long, variously curved, slightly tuberculate, tips rather obtuse.

Apothecia apical, up to 5 mm. in diameter, often subirregular; exciple smooth, subconvex; marginal cilia relatively abundant, erect at first, finally spreading, of variable length; disc concave at first, becoming nearly plane, carneous, white-pruinose; ascospores 9–11 μ in narrow asci.

Cortex about 30 μ thick, papery; medulla about 200 μ thick, very lax, white; axis 180 μ in diameter.

Our material from the Buddu District is evidently quite young, 2 (–3) cm. tall, the taller mostly once-dichotomous near the middle; apothecia cupulate with erect marginal cilia, only about 1 mm. in diameter, lateral near the tip, not strictly apical. Except for smaller dimensions, our plants agree quite well with Motyka's description translated above.

UGANDA: Buddu District, on twigs in sandy plain, 3950 [m. or ft.?], *H. U. Baul* [surname rather illegible], ex Bot. Gard. Entebbe, 1905; Kigezi, Kasatoro, in forest, 1930–2580 m., *I. R. Dale L39 p. p. min.*; both at Kew.

47. USNEA FUSCORUBENS Motyka, Lich. Gen. Usnea Stud. Monog. 546. 1937.

Type: Mauritius, without locality, *Simony*.

Thallus 6 cm. long, evidently subpendent, main axes Mars brown, secondary branches and ramuli russet; irregularly dichotomous throughout, axils about 90° angles; branches 1–1.5 mm. in diameter, irregularly curved, almost terete, sometimes deeply foveate, continuous or sometimes annularly cracked, verruculose-papillate, papillae short, cylindric, esorediose; ramuli distant, variously curved and branched, very slightly attenuate at the base, subinflated, almost smooth, the larger subtuberculate and subfoveolate, tips acute.

Apothecia about 6 mm. in diameter; exciple smooth, shining, the larger ones minutely papillate and foveolate; marginal cilia up to 10 mm. long, often branched, similar to the ramuli; disc slightly concave, densely white-pruinose.

The specimens from the Cape of Good Hope are somewhat larger, one about 7 cm. long, the other 12 cm. long, the lower joints about 2 mm. in diameter, and the apothecia of the shorter plant 8–9 mm. in diameter; in other characters, both macroscopic and microscopic, they agree well with Motyka's description translated above.

SOUTH AFRICA: Cape of Good Hope, without locality or collector, ex herb. Menzies in Tuckerman herb. sub *U. florida*, at Farlow Herb.

48. USNEA SUBMOLLIS Steiner, Verhandl. Zool. Bot. Ges. Wien 53:229. 1903.

Type: Cameroons, Fako, *Bornmüller*.

Thallus up to 5 cm. tall, simple or branched below, olive green (olive lake to ecru olive in our plants); holdfast indistinct, base not blackened, somewhat attenuate below, expanding to 0.6 mm. at the first branch; branching sympodial just above the base, branches somewhat constricted and annularly cracked at the base, inflated to 0.6 mm. in diameter in the lower third, then tapering to the tip; terete, not articulate, smooth or minutely and sparsely verruculose; ramuli not dense, about 1 mm. long, nearly perpendicular to the axis, bases articulate and slightly constricted, straight or slightly curved upward, slightly inflated, a few longer, up to 5 mm. long, with an occasional ramulus, perhaps aborted secondary branches; summits subulate.

Apothecia subterminal or lateral, sessile, 1.5 mm. in diameter, concave, exciple smooth; marginal cilia few (about 8), distant, suberect, resembling the small ramuli in size and shape; disc pale flesh color, white-pruinose.

Our Cameroons plants may be still immature as the dimensions are somewhat smaller than given by Motyka; the disc is covered by a white pruina. Our Nyasaland plants are a little larger than the type, the ramuli denser, and the apothecia up to 3 mm. in diameter.

CAMEROONS: Buea, 1290 m., on sticks on the ground, *F. W. H. Migeod 22*, at Kew.
CONGO: Mt. Minagongo, *D. H. Linder 2172*, at the Farlow Herb. and in Mo. Bot. Gard. Herb.

NYASALAND: Mlange District, Luchenya Plateau, Mt. Mlange, 1890 m., at forest edge, *L. J. Brass 16828, 16847* (Vernay Nyasaland Exp.), at N. Y. Bot. Gard. and Mo. Bot. Gard. Herbs.

SOUTH AFRICA: Cape of Good Hope, summit of mountain above Simon's Town on Simon's Bay, *Charles Wright* (Rogers & Ringgold N. Pacific Expl. Exp.), det. *U. barbata* v. *florida* by Tuckerman ex Gray Herb., at Farlow Herb.

49. USNEA BLEPHAROIDES Dodge, Ann. Mo. Bot. Gard. 43:395. 1956.

Type: Tanganyika, Kilimanjaro, at upper limit of forest, 3000 m., *G. Geilinger 4417*, at Kew.

Thallus fruticose, little-branched, prostrate or suberect, about 9 cm. long, axes drying tawny olive, ramuli and cilia cinnamon buff; holdfast broken off, subarticulate, lowest joint slender, tapering upward, more than 3 mm. long, 1 mm. in diameter below, expanding to 2 mm. above; joints constricted but cortex mostly continuous, with usually two lateral branches on the outer side of the curve of each joint, producing flexuous main branches, the last 3 mm. of the axes and all lateral branches unbranched, or with 1–2 secondary branches scarcely larger than ramuli but bearing minute apothecia; main branches 2 mm. in diameter below, tapering to 1 mm. under the apothecia, terete (somewhat crushed in the type), slightly verrucose (visible under 12× magnification), becoming minutely papillate on the joints just below the apothecia and at the bases of the larger ramuli; ramuli subdistant, 4–5 (–10) mm. long, curving upward, articulate and subinflated at the base, tips acuminate.

Apothecia 11–12 mm. in diameter, sessile on axes and slender branches, about 1.5 mm. from the tip, appearing terminal when mature, with concrescent ramuli forming low radial ridges, minutely verrucose (under 12× magnification); marginal cilia distant, up to 10 mm. long, curved, tips acuminate; disc flat, flesh color with a thin white pruina.

Cortex 85–125 μ, very variable in thickness, forming verrucae outside up to 60 μ tall and protruding as teeth between the algal colonies, 60 μ toward the medulla, outer 55 μ fastigiate, of conglutinate thick-walled hyphae 8 μ in diameter, lumen 2 μ, the rest of densely woven, predominantly periclinal thick-walled conglutinate hyphae, but the teeth between the algal colonies of radial hyphae, the outermost 15 μ nubilated with minute brown crystals; algal layer discontinuous, colonies about 30 μ in diameter, cells of *Trebouxia* 6–7 μ in diameter, closely packed; medulla about 375 μ thick, the outer portion (about 80 μ) densely woven, the rest of very loosely woven, predominantly radial hyphae 8 μ in diameter, lumen 3 μ, dichotomously branched; axis 250 μ in diameter, of longitudinal conglutinate thick-walled hyphae 3 μ in diameter.

This species differs from *U. blepharea* Motyka in having a larger axis, more gradually attenuated upper portions of the branches, fewer ramuli, an exciple without spinules, and a more regular disc. Perhaps the specimen from Kilimanjaro cited by Motyka belongs here rather than in *U. blepharea*, which is otherwise a Javan and Bornean species. Perhaps a single plant sorted out of *R. G. Turrall 55*

may also be this species. It is only 4 cm. tall, about 1 mm. in diameter below, surface not quite as verrucose and apothecium only 3.5 mm. in diameter.

TANGANYIKA: Kilimanjaro, at upper limit of forest, 3000 m., *G. Geilinger 4417*, type; 2930–3045 m., on twigs of giant heather in clearing in forest, *R. G. Turrall 55 p. p. min.*; both at Kew.

50. USNEA MOLLIUSCULA Stirton, Scottish Nat. 7:77. 1883.

Type: Australia, Victoria, subalpine country in upper Ovans River, *Mrs. McCann 1*, in Art Galleries of the Glasgow Corporation.

Thallus 6–7 cm. tall, fruticose, subflaccid, ochraceous tawny to buckthorn brown; holdfast about 3 mm. in diameter, of rootlike strands, dark, giving rise to 2–3 axes up to 2.3 mm. in diameter, somewhat attenuate but not blackened at the base; branching unequally dichotomous to sympodial, articulate, lowest joint nearly cylindric, about 5 mm. long, smooth, upper joints inflated, tuberculate to subpapillate, many papillae growing out as short, rather coarse spinules, sometimes in rows in the upper joints just under the apothecia, giving a somewhat foveolate appearance; ramuli sparse in the type, mostly 1–3 mm. long, a few up to 10 mm., annularly cracked and slightly inflated at the base.

Apothecia sessile, about 8 mm. in diameter, margins somewhat inrolled when dry; exciple smooth or somewhat reticulate-foveate; marginal cilia distant to irregularly close, very variable in length, up to 5 mm. long, tips acute, mostly broken off; disc white-pruinose; ascospores 9–11 × 7–8 μ.

In our South African material, the ramuli are irregularly dense, 2–3 (–10) mm. long, the longer annularly cracked in the middle and sparingly again ramulose. The apothecia are subterminal on short lateral branches, the exciple is smooth, the marginal cilia closer, shorter, and more inflated.

AUSTRALIA: Victoria, subalpine country of upper Ovans River, *Mrs. McCann 1*, in the Art Galleries of the Glasgow Corporation, a fragment in the British Museum.
CONGO: Mt. Kahusi, 2700 m., ramulicole, *F. L. Hendrickx 4308, 4314*, both in E. African Herb.
SOUTH AFRICA: Hermansdorp, Blue Lilies Bush, corticole, *A. Woodcock*, at Kew.

51. USNEA OBTUSATA Motyka, Lich. Gen. Usnea Stud. Monog. 622. 1938.

Type: Ethiopia, north slope of Mt. Kubbi, *Schimper*.

Thallus up to 8 cm. tall, fruticose, subrigid, dirty ashy greenish in herbarium (Motyka) but sepia shading to tawny olive in our material; base black, about 1 mm. in diameter, main axis rapidly expanding to 2 mm. and tapering upward to 1.5 mm. just below the terminal apothecium; lateral branches about 1 mm. in diameter, nearly perpendicular to the main axis but curving upward, subarticulate, slightly inflated, smooth or irregularly papillate (evidently very young ramuli); ramuli dense, perpendicular, mostly 1–2 mm. long, sometimes in longitudinal rows in the upper portion, giving a subrugose appearance, tapering from the base to a blunt tip, not articulate nor inflated, slightly curved upward.

Apothecia terminal (really subterminal, the tip of the branch concrescent with the exciple and protruding about 3 mm.); exciple smooth, with spines about 1 mm. long; marginal cilia close, about 3 mm. long, straight or slightly incurved, tapering to an acute tip, rather fragile; disc concave to somewhat deformed and coarsely rugose, flesh color (Motyka), tawny olive or darker in our material, white-pruinose.

Cortex 40–50 μ thick, of fastigiate pseudoparenchyma, thick-walled conglutinate cells, lumina 5–6 μ in diameter; algal layer 100 μ thick, cells densely packed under the cortex and next the medulla, more scattered between, protococcoid; medulla 300–360 μ thick, of very loosely woven, thin-walled hyphae 3–5 μ in diameter; axis solid, 160 μ in diameter, of vertical, thick-walled hyphae 2.5–3 μ in diameter.

51a. f. PERSTRIGOSA Motyka, Webbia 8:391. 1952.

Our material probably should be referred to f. *perstrigosa* Motyka, differing in strict, more acute ramuli, often very dense and paler fuscous The species was originally placed in the ALBOMACULATAE, but transferred by Motyka (*loc. cit.*) to the SETULOSAE, DENSIROSTRES. Although the original description calls for "sordide cinereo-viridulus," the description of the variety implies that the species is fuscous. Pseudocyphellae are not mentioned in the original description, hence the species does not belong in the ALBOMACULATAE. The thick, lax medulla, fuscous color in the herbarium, lack of papillae, and denser ramuli indicate a place in the GLABRATAE, CILIIFERAE, perhaps near *U. simplicissima*, rather than in SETULOSAE, DENSIROSTRES, with their thinner, very dense medulla and grayish green colors. Unfortunately I have not seen Motyka's types. The axis is relatively thinner than the dimension given by Motyka.

ETHIOPIA: Mulu, 20 miles north of Addis Ababa, 2580 m., *P. R. O. Bally 2078*, at Kew; Bagla, 2410 m., *Hildebrandt*, 1872, ex Herb. Sbarbaro, at Farlow Herb.

51b. f. PERFLAVA Motyka, Webbia 8:392. 1952.

Type: Ethiopia, Bacino del Tana, 2100–2200 m., *Pichi-Sermolli.*

Differs from the type in its yellowish fuscous color, especially in the upper part of the branches with golden yellow ramuli.

Chipp 57, from southern Sudan, seems to belong here. The main axis is tawny olive, the lateral branches shading to chamois and the ramuli colonial buff. The main axis is articulate, the joints more constricted at the ends; the apothecia are somewhat smaller, the marginal cilia less dense, and some of the longer ones branched.

SUDAN: Onyiro, Issare, 1770 m., 32° 50′ E., 3° 50′ N., *T. F. Chipp 57*, at Kew.

52. USNEA UNDULATA Stirton, Scottish Nat. 6:104. 1881, *non alio loco.*

Usnea foveolata Stirton, Scottish Nat. 7:77. 1883.
Usnea barbata v. *farinosa* Müll. Arg., Flora 74:373. 1891.
Usnea farinosa Zahlbr., Cat. Lich. Univ. 6:564. 1930.
Usnea Steineri v. *tincta* f. *sorediosa* Zahlbr., Bot. Jahrb. [Engler] 60:541. 1926.

Type: Bechuanaland, West Griqualand, Kimberley, *J. Shaw,* in Art Galleries of the Glasgow Corporation. Type of *U. foveolata* from same locality and collector in British Museum (Natural History). Type of *U. barbata* v. *farinosa* and *U. farinosa* from South Africa, *Peter MacOwan.*

Thallus 9 cm. or more long (up to 30 cm., *fide* Stirton), fruticose, pale ashy green, becoming buffy olive in the herbarium; holdfast of discrete, branched, flattened rootlets, not united into a disc, about 3 mm. long, rose color below where torn from the bark, buffy olive above; several times dichotomous just above the base, axils nearly 90° angles, the branches 1.5 mm. in diameter, curving and soon nearly parallel, flexuous and undulate, internodes longer above, rather densely covered with short ramuli, about 1 mm. long below, shorter and more slender spinules above; the more slender branches somewhat foveolate from minute isidiose soredia in rows, forming very slight anastomosing ridges (perhaps only scars of broken-off spinules); summits indistinct, mostly broken off.

Apothecia (absent in our plants) about 7 mm. in diameter, subterminal; exciple smooth or foveolate, with short spinules; marginal cilia very few, short, subulate; disc plane, white-pruinose; ascospores 4 × 8 μ, in narrow asci (*fide* Motyka).

A somewhat variable species, extending from Kenya to South Africa. Material from Kenya seems to be shorter with more spreading branches, some discolored reddish (about cameo brown), probably from too slow drying in the plant press. Ridges and foveolation are very indistinct in most of the plants, but are much more distinct in the type of *U. foveolata* and in *Dale 43* from Uganda.

KENYA: Chyulu Hills, *H. D. van Someren* (2 sheets in E. African Herb.); Lake Ngunga, 1775 m., on trees, *G. M. Allen 1838,* in Howe Herb. sub *U. florida* v. *strigosa* at Farlow Herb.; Nairobi, on trees, *G. M. Allen 1784,* in Howe Herb. sub *U. florida* v. *strigosa* at Farlow Herb.; Mt. Kenya, 3000 m., *Edgar A. Mearns 1776* (T. Roosevelt Exp.), ex herb. G. K. Merrill at Farlow Herb.

COMORO ISLANDS: Johanna Island, Pomoni lowland, on *Cocos* trunks, *Hildebrandt,* ex herb. Sbarbaro sub *U. barbata* f. *sorediata,* at Farlow Herb.

UGANDA: Kigezi, Kasatoro, Kabale R., 2250 m., arboricole, *I. R. Dale L43.*

CONGO: km. 30, route Kahusi, *F. L. Hendrickx 4330;* Mt. Kahusi, ca. 2700 m., *F. L. Hendrickx 4142, 4303, 4307, 4316;* all in E. African Herb.

NORTHERN RHODESIA: uplands of E. Isoka District, 1480 m., on tree in *Brachystegia mimosaefolia* scrub woodland, *C. G. Trapnell,* in E. African Herb.

BECHUANALAND: W. Griqualand, Kimberley, *J. Shaw,* in Art Galleries of the Glasgow Corporation, type of *U. foveolata;* same locality and collector, in British Mus. (Nat. Hist.).

SOUTH AFRICA: Cape of Good Hope, Uitenhage, forest near Zunday's River, *Zeyher,* in Taylor herb. sub *U. florida,* Ach., *a state?,* at Farlow Herb.

53. USNEA STRIGOSELLA Steiner, Bull. Herb. Boissier, II. 7:637. 1907.

Type: South Africa, Transvaal, Letaba District, Mt. Mamotsuri, *Henri A. Junod;* terminal fragment in Howe herb. at Farlow Herb.

Thallus pendent, about 30 cm. long, 0.6–1 mm. in diameter, slender, greenish stramineous, drying mikado brown or lighter on the main branches, ramuli and smaller branches cream buff; base short (absent in our plants), several times closely dichotomous below, axils acute, and again several times dichotomous with longer

internodes above, axils nearly right angles; spinulose and closely ramulose, terete, annularly cracked, sometimes slightly constricted at the cracks, sometimes not; smooth at first, often becoming spinulose and the surface uneven from the scars of the fallen spinules, sometimes slightly deformed where the spinules and small ramuli are arranged in close rows but not angular; ramuli close to dense, mostly about 2 mm. long, a few longer; summits short and indistinct.

Apothecia rare (absent in our plants), about 6 mm. in diameter, sublateral; exciple nearly plane, smooth; marginal cilia dense, radiating, of variable length, up to 12 mm. long, often annularly cracked; disc nearly plane, pale sulfur pruinose; ascospores 4 × 8 μ in narrow asci.

Cortex 65–100 (–115) μ thick, fastigiate, gelified, yellowish brown from minute crystals in the outer 65 μ, more hyaline within; algae in discrete colonies, about 30 μ in diameter, with smaller colonies scattered in the medulla; medulla variable, 65–190 μ thick, thicker where the cortex is thinner, rather compact except in a narrow zone next the axis where it mostly tears apart in sectioning, hyphae 6–7 μ in diameter, nubilated with granules, hyaline in outer portion, brownish in inner 30 μ next the axis; axis about 420 μ in diameter, transverse section somewhat irregular, of conglutinate, longitudinal hyphae 3 μ in diameter, with scattered cavities 7–8 μ in diameter, filled with brownish crystals and surrounded by a layer of thin-walled hyphae (reminding one of the resin canals of conifers).

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., *L. J. Brass 16847* (Vernay Nyasaland Exp.) in N. Y. Bot. Gard. Herb.
SOUTH AFRICA: Transvaal, Letaba District, Mt. Mamotsuri, *Henri A. Junod*, type fragment, com. Zahlbruckner, in Howe herb. at Farlow Herb.

54. USNEA PERSPINOSA Motyka, Lich. Gen. Usnea Stud. Monog. 2:533. 1937.

Type: Cameroons, mountain forest, 2200 m., *C. Ledermann.*

Thallus about 5 cm. tall, fruticose, spreading, rigid, green when fresh, drying fuscous (Isabella color to light brownish olive in our plants), ramuli lighter; holdfast low, conic, verrucose, not blackened, 4 mm. in diameter, base about 2 mm. long and wide and densely sympodially branched at the top, then less closely, but internodes short throughout; axils nearly right angles, main axis 2 mm. in diameter below, tapering to about 1 mm. below the apothecia; branches constricted at the base and often articulate, 1–1.5 mm. in diameter, terete, smooth to somewhat rugose from rows of spinules, in places appearing short-papillate from healing scars of the caducous spinules which are about 0.2 mm. long; cortex areolate, diffract in some places; ramuli up to 3 mm. long, annularly cracked at the base, slightly inflated and surface uneven, tips acute, often broken off.

Apothecia abundant, subterminal, sessile, cupulate, 2–3 (–10) mm. in diameter; exciple subfoveolate, densely spinulose; marginal cilia very dense, erect, inflated, up to 3 mm. long, tips forked, acute; disc very concave, white-pruinose.

The Uganda plants are somewhat variable; *Dale L69* is larger, nearly 7 cm. tall,

less densely branched, with one apothecium about 6 mm. in diameter; *Dale L. 85* has a few apothecia up to 10 mm. in diameter; *Dale L38* consists of plants smaller in all dimensions; *Dale L41 p. p.* has large apothecia but is shorter. The Kenya plants are paler and less densely branched, and the marginal cilia of the apothecia are shorter and more spreading. However, they seem closer to this species than to any other. *Mearns 508* has apothecia up to 18 mm. in diameter.

CAMEROONS: Cameroon Mt. above Buea, 2500 m., on dead decorticate shrub in grassland, *J. Milbraed 10838*, sterile and juvenile.

UGANDA: Bunyoro, Busingoro, on bark of Jacaranda tree, *I. R. Dale L69*; Kigezi, Mafuga, 2410 m., on trees, *I. R. Dale L41 p. p.*; Kasatoro, Kabale River, 2250 m., on trees, *I. R. Dale L43*; Kabale, 2000 m., on bush of *Hibiscus rosa-sinensis*, *I. R. Dale L55*; Fort Portal, on *Eucalyptus*, 1620 m., *I. R. Dale L38*; Fort Portal District, Toro, on trees, *I. R. Dale L40*; Mt. Elgon, 1290 m., *W. Small 217*; Bugishu, Bulambuli, on trees, *A. S. Thomas 548*, very young, all at Kew.

KENYA: Ngong, *H. D. van Someren 1948*, in E. African Herb.; Guaso Nyiro, *G. M. Allen 1792*, in Howe herb. sub *U. florida* v. *strigosa* Ach.; Narok River, 2000 m., *Edgar A. Mearns 508* (Theodore Roosevelt Exp.); both at Farlow Herb.

55. USNEA LUTEOLA Motyka, Frag. Florist. Geobot. 1:33. 1954.

Type: Madagascar, Manakambahiny Est, Marovato between Alaatra and Marovato, 800 m., com. des Abbayes.

Thallus up to 8 cm. long (5.5 cm. in our plants), caespitose, fruticose, subflaccid, pale yellowish to yellowish stramineous (axis Sayal brown, slender branches and ramuli chamois in our plants); holdfast of radiating, rather large, dichotomous, white rootlets, adhering to the bark and penetrating it at their tips; base not blackened, 1.2 mm. in diameter, 14 mm. long; about thrice dichotomous with relatively short internodes, axils nearly right angles but curving upward, divergent, not parallel; terete, rather densely covered with ramuli about 3 mm. long, and slender lateral branches up to 15 mm. long; cortex continuous or cracked but not articulate, the fertile branches tapering to about 0.5 mm. in diameter below the apothecia, sterile branches tapering to long-acuminate summits; main axes smooth except for small verrucae which develop to ramuli, the more slender branches papillate and tuberculate, the tubercles producing soralia with very few isidiose soredia, becoming farinose after the soredia are shed; ramuli rather dense, about 3 mm. long, with acute tips on the main axes and lower portions of the slender branches, mixed with coarser ones up to 10 mm. long (perhaps better considered as young lateral branches as they are tuberculate-sorediose); summits about 1 cm. long, tuberculate-sorediose, usually eramulose, sometimes forked above, tips acute.

Apothecia lateral, about 1 cm. below the tips of the branches, bending them downward, so that the apothecia appear subterminal, 3–5 mm. in diameter, nearly plane; exciple smooth; marginal cilia 2-ranked, the outer row subdistant, up to 10 mm. long, tuberculate-sorediate, the inner row short, 0.5–1 mm. long, closer; disc flesh color, covered by a dense white pruina at first, somewhat rugose.

MAURITIUS: Reduit, corticole, *G. Orian 3*, at Kew.

56. USNEA SULPHURASCENS Motyka, Frag. Florist. Geobot. 1:34. 1954.

Type: Madagascar, Manakambahiny Est, between Alaatra and Tanatave, 800 m., com. H. des Abbayes.

Thallus subdependent, flaccid, about 9 cm. long, sulfur yellow becoming ochraceous buff; base short, attenuate, indistinctly blackened; dichotomous to sympodially branched, axils nearly right angles, branches slightly constricted at the base, articulate, arcuate, axes 1–2 mm. in diameter, joints inflated in the middle, gradually tapering to the next articulation, terete, minutely tuberculate, tubercles bearing single white isidia and appearing pseudocyphelliform after the isidia are shed; summits slender, acuminate; apothecia not seen.

Cortex up to 40 μ thick, of coarse radial hyphae in a gel; algal layer 25–35 μ thick, cells *Trebouxia* ?, 6–7 μ in diameter in discrete colonies, forming a nearly continuous layer; medulla 125–150 μ thick, very compactly woven just under the algal layer, then very lax, of relatively thin-walled, branched hyphae, mostly 5–6 μ in diameter.

Our plant is ochraceous buff instead of stramineo-ochraceous, perhaps from having been much longer in the herbarium; the branching is more dichotomous on the larger axes; otherwise it agrees well with Motyka's description. Our plant is only 5 cm. long, but the lower portion has been broken off.

MADAGASCAR: without locality, *Dr. Moss*, March 1895, at Kew.

57. USNEA SYRIACA Motyka, Lich. Gen. Usnea Stud. Monog. 278. 1936.

Type: North Syria, Amanus near Beiland, on *Abies* at foot of Akma Dagh, 2600 m., *Kotschy*.

Thallus about 10 cm. long, fruticose, rather slender, pale ashy green, slightly fuscent in the herbarium, darker on the primary branches (main axes mikado brown, slender branches and ramuli cinnamon buff in our plant), opaque, base short, rather rigid, dark, infrequently branched from the base, axils nearly 90° angles or more acute; branches somewhat flexuous, about 1 mm. in diameter near the base, tapering gradually upward, terete, continuous or rarely simply annulate, the thicker branches shortly and densely papillate, the more slender branches less so, forming very obtuse ridges, the backs decorticate and farinose, evidently producing soredia as well as the tips of some papillae; ramuli not close, mixed longer and shorter, very thick at the base, tapering gradually upward; summits rather long, farinose, so that they appear whitish.

Cortex 60 μ thick, rather hard and elastic, pale; medulla about 150 μ thick, white, dense, K intensely reddening; axis 330 μ in diameter with some dark hyphae.

Our plant from Eritrea agrees more closely with Motyka's description translated above than with any other, but the medulla is K—. The base is absent and the axis blackened about 2 cm. and up the secondary branches, suggesting that it is prostrate and the axis covered with leaf mold, in which case it may be much longer and the portion collected only the terminal portion. The cortex regenerat-

ing in the annular cracks shows as white rings about the lower portions of the secondary branches. The soralia are well developed, slightly elevated, producing granular soredia, in some places so crowded as to form almost continuous areas. The proportions of cortex, medulla and axis are nearly the same, but the absolute dimensions are nearly double. The structure of the cortex is unusual, being formed of interwoven and anastomosing hyphae with moniliform lumina, leaving entrapped minute air bubbles (seen in freshly mounted sections), suggesting the spongy cortex of the subgenera LETHARIELLA and CHLOREA. The algae occur as small colonies throughout the moderately lax medulla, not forming a separate layer between the cortex and medulla. The algal cells seem to be short, discrete cylinders, although packed in rounded colonies, suggesting that they may have come from filaments of *Trentepohlia* with nearly isodiametric cells, occasionally more filamentous as they push out along cracks in the cortex. The axis is solid and quite uniform with an occasional small bundle of brownish hyphae in the outer 50 μ.

Motyka mentions a plant from Anatolia, Ibidh dere, *H. Czeczott*, at Cracow, which has a solid axis and a K— medulla, tentatively referred to *U. syriaca*. Our plant may be a distinct species, but I dislike to describe a new taxon on a single incomplete plant.

ERITREA: without locality, *F. Gallina*, ex herb. Sbarbaro sub *U. plicata*, at Farlow Herb.

58. USNEA SUBLEPROSA Motyka, Lich. Gen. Usnea Stud. Monog. 605. 1938

Type: South Africa, Transvaal, Lydenburg, *Wilms*.

Thallus up to 20 cm. long, usually smaller (7 cm. in our plant), rigid, perhaps pendent, subglaucescent drying olive green (Motyka), (fuscous on larger branches shading to dark olive buff at the summits and ramuli in our plants); base penetrating crevices in the rock (broken off in our plants); lower portion about 1.5 cm. long, 1.5 mm. in diameter, black, forming an arc of about 90°, sympodially branched with very short internodes; principal axes flexuous, articulate, joints constricted at the ends, slightly inflated in the middle, up to 2 mm. in diameter below, of variable length, rarely annularly cracked, densely verrucose to subpapillate, the more slender lateral branches subarticulate, verrucae less dense and larger, forming slightly elevated soralia of isidiose soredia which appear farinose after the soredia are shed; ramuli subdistant, about 10 mm. long, curving toward the summits, verrucose and sorediose, slightly constricted at the base, annularly cracked, inflated in the lower portion, tapering to a short obtuse tip, often broken off; summits about 20 mm. long from dichotomy of the axis or lateral branch, about 0.5 mm. in diameter, resembling ramuli in structure.

Apothecia rare (absent in our plants), lateral to subterminal, up to 7 mm. in diameter; exciple uneven, sublacunose, verruculose and sorediose, sometimes ciliate; marginal cilia few or none, about as long as the diameter of the disc, rather thick,

obtuse, subarticulate, with farinose soredia; disc plane or somewhat deformed, flesh color, slightly or not pruinose.

KENYA: Guaso Nyiro, *G. M. Allen 1792 p. p.*, in Howe herb. sub *U. florida* v. *strigosa* Ach., at Farlow Herb.

CONGO: Mont Kahuz, about 3000 m., saxicole, *F. L. Hendrickx 1273*.

PORTUGESE MAIOMHE: Chiluango, *J. Gossweiler* (1919); rather young, papillae in dense longitudinal rows on some branches, not on others, giving an angular appearance.

59. USNEA LEDIENII (Stein) Motyka, Lich. Gen. Usnea Stud. Monog. 593. 1938.

Usnea strigosa v. *Ledienii* Stein, Jahresber. Schles. Ges. Vaterl. Cultur 66:139. 1888.

Type: Cameroons, Buea near the caves, *Preuss*.

Thallus fruticose, erect, rigid, about 7 cm. tall, drying citrine drab, more slender branches and ramuli dark olive buff; base 3 mm. in diameter, a dense mass of root-like fibers penetrating the bark, slightly darker; densely sympodially branched at the base and rarely dichotomous above, branches up to 1.5 mm. in diameter below, tapering gradually upward, remaining rather thick to the summits, somewhat flexuous, slightly attenuate and articulate at the base, not or only very slightly articulate above, with simple annular cracks; terete, sparsely and irregularly tuberculate to subpapillate below, more closely so above, tubercles sometimes in rows but not close enough to form ridges, forming soralia of isidiose soredia, especially on the more slender branches and larger ramuli; ramuli quite close, some 1–3 mm. long, smooth, others up to 15 mm. long, tuberculate and sorediose, sometimes so densely so that they appear furfuraceous, axils right angles but the longer ramuli curve upward, flexuous.

Apothecia not abundant, subterminal on the main axes, up to 10 mm. in diameter, often deformed; exciple plane or deformed, smooth when young becoming uneven and foveolate or scrobiculate; marginal cilia not close, long and short intermixed, rarely longer than the diameter of the disc, relatively thick, the longer tuberculate and with secondary ramuli; disc nearly plane or deformed, chalky white pruinose; ascospores 7–10 μ in narrow asci.

The above description of apothecia is translated from Motyka, *loc. cit.*, as only a single young apothecium is present in our material.

CAMEROONS: forest above Buea, 1450 m., *F. W. H. Migeod 144 p. p. min.*

ANGOLA: Cuanza Sul, Amboim, Capir, near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991*; Benguella, country of the Ganguellas and Ambuellas, *J. Gossweiler*; both at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., *I. R. Dale L43*; Mt. Elgon, 1290 m., on trees, *W. Small 218*; both at Kew.

60. USNEA HISPIDA Motyka, Lich. Gen. Usnea Stud. Monog. 589. 1938.

Type: Cameroons, "Huea" (*lapsus calami* for Buea?), corticole, *Lemperch*.

Thallus probably pendent, rather rigid, up to 15 cm. long, drying sepia to bone brown, the ramuli lighter, cinnamon buff; holdfast black, thin, very rugose, 5–6 mm. in diameter, nearly surrounding a small twig; base very short, rigid, sym-

podially branching into 8–10 branches which bend around the twig and hang down on both sides; about thrice dichotomous in the basal portion with internodes about 10 mm. long, rarely dichotomous near the summits; branches straight or slightly curved, with annular cracks in the basal internodes, then articulate in the middle portion of the principal axes, joints constricted at the ends, slightly inflated, 1.5–2 (–3) mm. in diameter, thinning at each dichotomy, the more slender branches annularly cracked but not distinctly articulate; surface with very dense long papillae with a few areas sparsely so; ramuli subdistant on the larger joints, rather close on the more slender branches, 2–10 mm. long (some longer and themselves ramulose may be young lateral branches), the shorter smooth, the longer low-tuberculate, tips acute to acuminate; summits short, slender with subterminal apothecial initials.

Apothecia abundant, mostly about 5 mm. in diameter, a few up to 10 (–15) mm., sessile about one third the way from the tip of stout ramuli or small lateral branches, cupuliform becoming plane or rarely revolute; exciple smooth or in very large apothecia with a few radial ridges and sparsely tuberculate; marginal cilia few, radiating, 3–4 mm. long, quite fragile, tips acute; disc concave to plane or somewhat convex, densely white-pruinose, becoming snuff brown in age.

In *Hendrickx 3679*, the apothecia are much larger than usual, the marginal cilia are closer and longer (up to 20 mm. long), exciple with occasional short ramuli or large spinules on some of the larger apothecia, not on others of equal size. There are suggestions that some of the papillae grow out to form small spinules which easily break off as propagula. The colors are lighter, perhaps because more recently collected.

CAMEROONS: Cameroon Mt., 390 m., *Collier 1169*, ex herb. Bot. Gard. Victoria; in Meyer Crater, 1930 m., on *Aquaria salicifolia*, *T. D. R. 917*, ex herb. Bot. Gard. Victoria; above Buea 1290 m., ramulicole, *F. W. H. Migeod 53*; all at Kew.

FERNANDO PO: [Santa Isabel Peak], 1610 m., *Gustavo Mann 682* (two plants, tangled with summits of *U. speciosa* and *Anaptychia leucomelaena*, glued to sheet, making it difficult to trace branching), at Kew.

SÃO THOMÉ: *Gustavo Mann*, at Kew.

CONGO: Route Kahusi, 2450 m., on *Hagenia*, *F. L. Hendrickx 3679*, in E. African Herb.

61. USNEA OCHROPHORA (Stzbgr.) Motyka, Lich. Gen. Usnea Stud. Monog. 254. 1936.

Usnea florida v. *ochrophora* Stzbgr. in herb.

Type: South Africa, Cape of Good Hope, Talbe Mt., *Peter MacOwan*.

Thallus erect, rather rigid, up to 10 cm. tall, ashy green, drying between Saccardo's umber and buffy brown on main axes, lateral branches and ramuli wood brown to avellaneous; holdfast a dark disc about 2.5 mm. in diameter, base 1 mm. in diameter below expanding to 1.5 mm. above, 2 mm. tall, branching sympodial with short internodes in the lower half; axils of lower branches 90°, upper acute;

main axis 1.5 mm. in diameter below, tapering to 0.5 mm. below the subterminal apothecium; subarticulate, joints very slightly inflated, annular cracks wide, exposing the medulla; lateral branches similar but only 0.8 mm. in diameter, slightly constricted at the base, quite closely and minutely papillate throughout, a few papillae growing out as short spinulose ramuli; ramuli subdistant, about 5 mm. long, tips acuminate, paler, bases slightly constricted and articulate, slightly inflated and minutely tuberculate, rarely with a secondary ramulus, rather fragile.

Apothecia 4–5 mm. in diameter, sessile to subterminal on the main axis and lateral branches, cupulate becoming plane; exciple smooth to slightly rugulose with a few papillae near the point of attachment; marginal cilia subdistant, radiating, 2–7 (–10) mm. long, sometimes forked near the base, similar to ramuli; disc concave to plane, chalky-pruinose.

SOUTH AFRICA: Cape of Good Hope, Hermansdorp District, Blue Lilies bush, *A. Woodcock*.

NYASALAND: Nyika plateau, 2340 m., ramicole, *L. J. Brass 17212*, in N. Y. Bot. Gard. (Vernay Nyasaland Exp.)

TANGANYIKA: S. Pare Mts., Mt. Mtonto, 2100 m., ramulicole, in evergreen forest of steep slopes, *P. J. Greenway 6532*.

CONGO: Mt. Kahusi, ca. 2700 m., ramulicole, *F. L. Hendrickx 4300*, in E. African Herb.

KENYA: Mt. Kenya, 2250–2575 m., on bamboo twigs, *G. M. Allen* (only 4 cm. tall, cinnamon buff to pinkish buff, apothecia wholly lateral).

UGANDA: Kigezi, Mafuga, 2410 m., *I. R. Dale L41 p. p. min.* (only 4.5 cm. tall with single lateral branch and immature apothecia).

ERITREA: without locality, *F. Gallina*, ex herb. Sbarbaro sub *U. plicata*, at Farlow.

62. USNEA SUBFOVEATA Dodge, Ann. Mo. Bot. Gard. 43: 395. 1956.

Type: Uganda, Bunyoro, Busingoro, on bark of *Jacaranda, I. R. Dale L69*, at Kew.

Thallus fruticose, erect, rigid, 5 cm. tall, between buffy olive and yellowish olive when dry; holdfast 3 mm. in diameter, not blackened, giving rise to three main axes, 1–1.5 mm. in diameter; closely dichotomous, branches slightly curved, axils 60–90°; articulate, joints about 10 mm. long, constricted at the ends, often bearing one or more lateral branches to a joint, more slender than the main axis, terete, subfoveolate from ridges of small papillae, many of which produce 1 or 2 spinulose isidia which break off, leaving a decorticate tip to the papilla; eramulose (small fragile lateral branches sometimes simulate ramuli).

Apothecia subterminal on the main axis and lateral branches, up to 9 mm. in diameter (often 2 develop less than 1 mm. apart so that the exciples are in contact but not concrescent), cupulate becoming plane, smooth to slightly impressed and verrucose or the larger ones few-ciliate; marginal cilia distant, up to 1.5 mm. long, annularly cracked and slightly constricted at the base, inflated in the middle and tapering to a subacute tip; disc concave to plane, smooth (deeply scrobiculate from folding of the thecium, teratological ?), ochraceous buff with a thin white pruina.

Cortex 30 μ thick, outer half brownish, closely fastigiate, inner half hyaline, hyphae more loosely interwoven, lumen about 2 μ; the whole in a gel; algal layer 15–20 μ thick, continuous, cells protococcoid, 6–8 μ in diameter; medulla 360 μ thick, the outer 35 μ densely woven, the rest almost wholly radial, of about 36 hyphae per circumference, dichotomous outward, very thick-walled, 5–6 μ in diameter, lumen 1 μ; axis 220 μ in diameter, solid, hyaline, of conglutinate, thick-walled hyphae.

This species is suggestive of *U. cristata*, which is more angled with a much larger hollow axis. *U. complanata* (FOVEATAE) has a thicker, complanate thallus without articulations or isidia and is partly ramulose. *Turrall 55 p. p. min.* is apparently a small moribund specimen, only about 2 cm. tall with apothecia 2 mm. in diameter.

SUDAN: without locality, *J. T. Bent*, at Kew.
KENYA: Northern Frontier Province, summit of Ajao hill, 1030 m., near Buna, on bushes, *I. R. Dale L71*; Mau Forest, Endabarrá, 2350 m., at edge of *Acacia* grove, on trees, *P. R. O. Bally B4947*, a small fragment; all at Kew.
UGANDA: Bunyoro, Busingoro, on bark of old *Jacaranda* tree, *I. R. Dale L69*, type, at Kew.
TANGANYIKA: Kilimanjaro, 2900–3045 m., on giant heather in clearings, *R. G. Turrall 55 p. p. min.*, at Kew.

63. USNEA TRACHYNA Motyka, Lich. Gen. Usnea Stud. Monog. 612. 1938.

Usnea barbata v. *aspera* Müll. Arg., Flora 73:336. 1890, *non alio loco.*

Type: Tanganyika, Pagani, *von Hoehnel*, at Turku.

Thallus in type specimen 7 cm. long (incomplete, in other specimens cited by Motyka shorter, fruticose, in our plants about 6 cm. tall), somewhat prostrate, subflaccid, ashy olive green (*fide* Motyka, in our plants warm sepia to Verona brown, ramuli wood brown); holdfast a disc 2 mm. in diameter, scarcely darkened, base 3 mm. tall, 1 mm. in diameter below, expanding to 2 mm. just under the first branch; branching sympodial or more often unilateral, the axis and first branch curving downward and apparently nearly prostrate, the other branches erect, axils nearly right angles; articulate, joints variable in length, ends constricted to 1 mm. in diameter or less, inflated to 1.2–1.5 mm. below, to 1 mm. just below the apothecia; terete, papillae subdistant below, rather close above, small, short-cylindric, or larger, subcapitate or somewhat coralloid (perhaps from regeneration after small ramuli have broken off as the tips are more or less decorticate); ramuli quite close, mostly broken off on the older joints, 1–10 mm. long, the shorter smooth, but annularly cracked, the longer tuberculate to small-papillate, the longest with secondary ramuli (probably young lateral branches).

Apothecia subterminal on lateral branches (often appearing terminal when the end of the branch has broken off), 5–8 mm. in diameter, nearly plane, but margin somewhat inrolled and folded in drying; exciple smooth, subfoveolate and partly minutely papillate on the larger ones; marginal cilia subdistant, 3–4 mm. long,

similar to ramuli but very fragile and mostly broken off, leaving only a few short young cilia; disc plane, pale olive buff pruinose.

Ellis 4 is rather short, 3–4 cm. tall, with a thinner cortex (40–55 μ) but agrees otherwise. *Dale L40* is 4 cm. tall, more erect and densely ramulose, although it is abundantly fertile with apothecia up to 7 mm. in diameter.

ERITREA: Filfa Pass, *P. E. Ellis 4*, at Kew.
KENYA: Chyulu Hills, *H. D. van Someren*, in E. African Herb.
UGANDA: Toro, Fort Portal, 1630 m., *I. R. Dale L40*; Kigezi, Mafuga, 2410 m., *I. R. Dale L41 p. p.*; both at Kew.
TANGANYIKA: Kilimanjaro, Marangu-Bismarck, 2100 m., *R. G. Turrall 37*, at Kew; Maruessa, *Hildebrandt*, ex Herb. Sbarbaro, at Farlow Herb.

64. USNEA SCUTATA Motyka, Lich. Gen. Usnea Stud. Monog. 602. 1938.

Type: Cameroun Française, Ntem, 950 m., *Ledermann*.

Thallus fruticose, rigid, dirty glaucescent olive green (light brownish olive shading to Isabella color on slender branches and ramuli in our plants), attached by rooting fibers which penetrate the outer layer of the bark, without a visible holdfast, base about 3 mm. tall, 1 mm. in diameter below, expanding to 2 mm. at the first branch, rarely unbranched below, tapering gradually to 1 mm. in diameter below the apothecium; once or twice dichotomous above the base with very short internodes, then unequally dichotomous above, axils about 90°; articulate, the joints inflated, ends constricted, rather long, bearing 3–4 lateral branches 1 mm. or less in diameter, usually terminated by apothecia, a few sterile ones ending in a tuft of 3–4 slender branches about the size of the larger ramuli but minutely ramulose; terete, verruculose-papillate, very few papillae on the lower joints, denser above on low reticulate ridges and the surface appearing subfoveolate, some of the more cylindric papillae growing out as minute ramuli, leaving scars as they break off, but not sorediose; ramuli irregularly disposed, rather dense on some branches, distant on others, 2–3 mm. long, tips obtuse, annularly cracked and subinflated, smooth, some probably developing as small lateral branches, minutely papillate and minutely ramulose.

Apothecia subterminal, cupulate becoming plane, up to 15 mm. in diameter; exciple densely verruculose-papillate; marginal cilia in two ranks, distant, 2–3 mm. long, resembling ramuli; disc flesh color, covered by a dense white pruina.

Our material agrees well with Motyka's description except the apothecia are only 3–5 mm. in diameter and the disc is concave. *Deighton 3503* has more dense ramuli and the papillae in less distinct rows. *Allen 1779* from Kenya is larger in all dimensions but otherwise agrees. Thallus 10 cm. tall, rather flaccid; apothecia up to 23 mm. in diameter; cortex 130 μ thick, highly gelified, outer 20 μ deep brownish, of very loosely woven, predominantly radial hyphae, denser just below the colored zone; algal layer about 70 μ thick, of colonies of *Trebouxia*, forming a nearly continuous layer; medulla 670 μ thick, of very loosely woven thick-walled hyphae 6–7 μ in diameter, predominantly radial and somewhat more densely woven in a narrow zone just below the algal layer; axis 410 μ in diameter, solid, of longi-

tudinal, relatively thick-walled hyphae, lumen about 3 μ, becoming brownish in age. The large size is suggestive of *U. ruvidescens*, but the proportions of cortex, medulla and axis are nearer those of *U. scutata*, as are the conspicuous papillae.

SIERRA LEONE: Lei, Sankon Biriwa, 1930 m., *F. C. Deighton 3503*, at Kew.
ANGOLA: Northeast Lunda, Dundo, 750 m., near the Luachima River, on tall trees of the gallery wood, *J. Gossweiler 13928*, at Kew.
KENYA: Lake Ngunga, 1770 m., on branches of trees, *G. M. Allen 1779*, in Howe herb. at Farlow Herb.

65. USNEA ALBOMACULATA Motyka, Lich. Gen. Usnea Stud. Monog. 620. 1938.

Type: Ethiopia, Isaac Debr., Semenbachgebirge, *Stender*.

Thallus pendent, 7–9 cm. long, probably olive buff or lighter when living, larger branches between wood brown and dark olive buff, slender branches and ramuli olive buff or pale olive buff after 3 years in the herbarium (pale fuscous after 75 years); holdfast conic, about 2.5 mm. in diameter, of radiating, concrescent blackened root-like fibers, base 1 mm. in diameter below expanding to 1.5 mm. above, about 3 mm. long; branching unequally dichotomous below, closer and more sympodial above; articulate and 1.5 (–2.5) mm. in diameter below, tapering to about 1 mm. and scarcely articulate below the apothecia, with minute indistinct verrucae and large pseudocyphelliform elevated white ecorticate tubercles (apparently from regeneration where a small branch has broken off from unusually great proliferation of the medulla, not truly farinose-sorediose), round or somewhat oblong, more closely verrucose to minutely tuberculate above and subfoveate just under the apothecia; ramuli dense on the smaller branches, 2–8 mm. long, ascending (the longer perhaps young branches as they are verruculose at the base and sometimes branched above), articulate and constricted at the base, inflated, tapering to an acute tip.

Apothecia sessile on the smaller branches as well as terminal, 4–6 (–15) mm. in diameter, concave; exciple smooth or subpapillate near the base with a few small ramuli; marginal cilia close, thick, conic, slightly constricted at the base with acute tips, in two rows, the outer longer, sometimes branched, the inner shorter, simple; disc concave, flesh color, slightly white pruinose.

Chipp 57 p. p. is tentatively referred here although the surface is almost papillate, the ramuli are less dense, and the white pseudocyphelliform tubercles are smaller and rarer.

ETHIOPIA: Simien, Mindigabsa, ramulicole, *H. Scott 323*, at Kew.
SUDAN: Onyiro, Issore, 1770 m., 3° 50′ N., 32° 50′ E., *T. F. Chipp 57 p. p.*; Mt. Kinnelli, on pole and cairn, 3360 m., *T. F. Chipp 64*, juvenile, tangled with *U. maculata* Stirton, both at Kew.

66. USNEA BORNMUELLERI Steiner, Verhandl. Zool. Bot. Ges. Wien 53:227. 1903.

Type: Cameroons, Cameroon Mt., *Alfred Bornmueller*, portion of cotype in Howe herb. com. Zahlbruckner, at Farlow Herb.

Thallus suberect to prostrate, 5–8 cm. tall, somewhat flaccid, "gelblich-graugrun" (Milbraed) when fresh, drying olive green (Motyka) but brownish olive below shading to Isabella color in our plants; holdfast subhemispheric, 3 mm. or more in diameter, black, the root-like fibers broken in collecting; main axis 1 mm. in diameter, rapidly expanding to 2 mm., closely dichotomous near the base, then less frequently so in the upper portion and again very closely so at the summits, axils nearly 90° angles; branches somewhat curved, articulate, joints inflated up to 2.5 mm. in diameter in lower portion, tapering to 0.5 mm. just below the tips, 5–12 mm. long, terete, cracked between the joints but not separated (unless roughly handled in collecting); surface irregularly verrucose, sometimes in short ecorticate ridges on the lower joints, with somewhat larger, low tubercles on the upper joints, producing isidiose soredia which soon break off, leaving white punctiform scars, the larger ones resembling small farinose soredia; summits densely branched, somewhat deformed by small tubercles, not soraliate, tips blackened (much less so than in species of the subgenus *Neuropogon*).

Cortex 60 μ thick, brownish, gelified, very hard, fastigiate, lumen of hyphae about 1 μ; algae in scattered discrete colonies, about 35 μ in diameter, cells protococcoid, 6–7 μ in diameter; medulla about 980 μ thick, of very loosely woven hyphae 6–7 μ in diameter, lumen 1 μ, periclinal next the algal colonies and cortex, radial within; axis 200 μ in diameter, outer surface slightly irregular, of thick-walled longitudinal, conglutinate hyphae.

CAMEROONS: Cameroon Mt., grasslands, *Alfred Bornmueller*, portion of type, com. Zahlbruckner in Howe herb. at Farlow Herb.; mountain above Buea, 3900 m., saxicole, in grasslands above tree line, *J. Milbraed 10913*, at Kew; 1500 m., *F. W. H. Migeod 144*, at Kew; 400 m., *Pollier 1169bis*, at Kew.

67. USNEA FLOTOWII Zahlbr., Bot. Jahrb. [Engler] 60:541. 1926.

Usnea barbata v. *cornuta* Flotow, Linnaea 17:16. 1843, *p. p.*

Type: Ethiopia, Mont. Simens., 3000–4000 m., saxicole, *Schimper*.

Thallus caespitose-fruticose, suberect, about 10 cm. tall, rigid; base hemispheric, 5 mm. in diameter, sympodially branched about 2 mm. above, forming prostrate principal axes from which arise erect lateral branches on the upper side, very close in the proximal half of some axes, less so in others; lateral branches dichotomous, some once, others several times, especially in the upper portion, making a very intricate mass; main axes and secondary branches 2 mm. in diameter, tapering at each dichotomy to short, slender summits; articulate on main axes and secondary branches in lower portions, joints constricted at the ends, somewhat inflated, simply cracked above, surface closely and minutely white-tuberculate except the basal joints, the tubercles often in rows, forming reticulations or, where longitudinal, appearing slightly angular, mostly forming soralia of isidiose soredia; most axes and secondary branches eramulose, a few densely to sparsely ramulose; shorter ramuli 1–2 mm. long, nearly smooth, the larger 10–15 mm. long, coarser,

more fragile, a few branched, closely tuberculate to subpapillate, producing soredia; summits short, obtuse, rugose, farinose from soredia.

Jarrett 402 is a single moribund fragment closely related to this species but may be new. It is in too poor condition to describe; it is arboricole and comes from a much lower altitude.

ETHIOPIA: Simien, Mindigabsa, *H. Scott 323 c*, moribund fragments, portions in Howe herb. com. Zahlbruckner, at Farlow Herb.
KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.
UGANDA: Kigezi, Muhavura, 4230 m., saxicole, among mosses, *A. S. Thomas 1114*; Ruizi River, 1390 m., arboricole, *T. Jarrett 402*; both at Kew.

68. USNEA SERPENTARIA Motyka, Webbia 8:392. 1952.

Usnea Flotowii subsp. *serpentaria* Motyka, Lich. Gen. Usnea Stud. Monog. 625, 1938.

Type: Ethiopia, Mont. Simens. near Dibell, saxicole, 3000–4000 m., *Schimper.*

Thallus erect, forming dense tufts, 9 cm. tall from a common holdfast, up to 9 mm. in diameter with dense dichotomously branched root-like fibers about 2 mm. long; branches simple or dichotomous just above the base, often again dichotomous about 1 cm. above the base and again about 3 cm., then more frequently dichotomous, the ultimate branches sparingly ramulose; base blackened to the first dichotomy, shading upward from Saccardo's umber through buffy citrine to old gold at the summits and ramuli; branches 2 mm. in diameter below, slightly flexuous, thinner at each dichotomy, ultimate branches and ramuli 0.2–0.3 mm. in diameter at the base, tapering upward to obtuse, dark brown tips, not articulate nor inflated, subfoveate with low flat ridges, cortex subareolate but not flaking off on the larger branches, the smaller branches less rugose and sparsely papillate, the papillae short and broad, forming minute pseudocyphellae on all but the slender ramuli; ramuli rare or absent on some branches, unilateral on others, varying from 2 to 20 mm. long, curved upward. Only one moribund subterminal apothecium present in our plants.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.

69. USNEA CAPENSIS Motyka, Lich. Gen. Usnea Stud. Monog. 321. 1937.

Type: S. Africa, Orange Free State, Taaboschkranz, *Rehman.*

Thallus caespitose-fruticose, erect, about 5 cm. tall, pale ashy olive green (buffy olive in our plants); holdfast a black cone, 4 mm. in diameter, 2 mm. high, adherent to the rock, giving rise to about two axes 1.5 mm. in diameter, expanding to 2 mm. at the lowest dichotomy, rather closely but unequally dichotomous throughout; articulate, joints constricted at the ends, subinflated below, relatively long, tapering upward but relatively thick to the summits, subareolate below, smooth above (very faintly verrucose under 12× magnification); ramuli very dense but very fragile, up to 5 mm. long, tips acute, often blackened but more

often broken off and then digitiform, slightly constricted at the base, subinflated, densely beset with minute spinules with blackened tips near the summits; summits finally curved, 0.2–0.3 mm. in diameter, grossly tuberculate with isidiose soredia, appearing farinose after the soredia are shed. Apothecia not seen.

Thomas 3631 is smaller, about 4 cm. tall, and very few of the sorediose recurved summits have been formed, evidently the decadent spinules serving as isidia. The *Forbes* specimen from Nyasaland is 5 cm. tall and more sparingly branched; it may be a juvenile form of *U. transvaalensis*, although it agrees in other vegetative characters with *U. capensis*.

UGANDA: Karamoja, Napak, 2250 m., on rocks in mountain grassland, *A. S. Thomas 3631*, in E. African Herb.

NYASALAND: Mt. Mlangi, 1930–2250 m., *A. P. S. Forbes* (6 July 1939), in E. African Herb.

SOUTH AFRICA: Cape of Good Hope, without locality, *Mund & Maire*, in Tuckerman herb. sub *U. barbata* v. *hirta*, at Farlow Herb.

70. USNEA PULVINATA Fries in Lehmann, Pl. Preiss. 2:145. 1846-47.

Type: Western Australia, *Preiss*.

Thallus up to 3.5 cm. tall, erect, fruticose, very rigid, pale greenish, drying olive ochre to honey yellow in the herbarium; holdfast of coarse radiating rootlets penetrating between the rock crystals, somewhat blackened and verrucose; branching into three or more primary axes about 1 mm. in diameter, lowest internode variable in length, up to 8 mm., then twice or thrice closely dichotomous and rarely so above, angles about 45° and the branches curving upward, terete, surface smooth except for scars of broken ramuli; ramuli variable in length, 1–10 mm. long, slightly constricted at the base and inflated in the middle, about 0.2 mm. in diameter, curving upward and tapering to obtuse tips, some growing out as slender lateral branches and again short-ramulose, surface tuberculate, forming small soralia of isidiose soredia, usually black-tipped and appearing farinose after the isidia are shed, in old plants the soralia more or less confluent, giving a furfuraceous appearance under 12× magnification.

Apothecia absent in our material, reported by Motyka as terminal, about 3 mm. in diameter; exciple smooth, sometimes with tubercles; marginal cilia short, dense, thick and obtuse; disc somewhat concave, yellowish flesh color, slightly pruinose.

Cortex about 110 μ thick, fastigiate and brownish in the outer 30 μ, loosely and irregularly woven below, imbedded in a hyaline gel; algal layer of discrete colonies of *Trebouxia*, about 30 μ in diameter, forming a nearly continuous layer, cells 4–7 μ in diameter, somewhat polyhedral from mutual pressure; medulla 75–80 μ thick, white, K—, densely woven, of predominantly periclinal hyphae 6–7 μ in diameter, lumen 1 μ, inner 10–15 μ brown next the axis; axis 700 μ in diameter, outer 200 μ of interlaced transverse hyphae, predominantly periclinal, the central cylinder predominantly of longitudinal hyphae with more slender lumina and much more transparent so that under lower magnifications the axis appears hollow.

The Robillard plant is somewhat doubtfully referred here, as the cortex and axis are thinner and the soredia are less developed. The axis is uniformly composed of longitudinal hyphae.

MADAGASCAR: Imerina, Andrangoloaka, saxicole, *Hildebrandt 2172* (3 collections), at Farlow Herb., Province of Betafo, *native collector*, spring 1901, ex herb. E. G. Paris, 1904 (2 specimens), at Farlow Herb.

MAURITIUS: without locality, *Robillard* ex Gray Herb. sub *U. florida* v. *strigosa* Ach., at Farlow Herb.

71. USNEA MYRIOCLADA (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 6:588. 1930.

Usnea barbata v. *myrioclada* Müll. Arg., Bot. Jahrb. [Engler] 20:244. 1894.

Type: Tanganyika, Usambara, Derema, *Fischer*.

Thallus erect, subfruticose, about 5 cm. tall, pale glaucescent green (Motyka, axes between buffy brown and citrine drab, ramuli between dark olive buff and deep olive buff in our plants); base of coarse rooting fibres penetrating dead wood; closely sympodially branched at the base and frequently so throughout, axils nearly right angles, becoming nearly dichotomous below the summits; main axes subarticulate, joints very slightly inflated, rather long, very densely ramulose below, appearing smooth between the ramuli but slightly verruculose under 36× magnification; ramuli mostly 1–2 (–5) mm. long, slightly constricted at the base, annularly cracked, slightly inflated, fragile, many broken off at the base, giving a coarsely verrucose appearance, abruptly tapering to an acute black tip; slender branches and summits nearly devoid of ramuli, closely tuberculate, producing soralia of isidiose soredia which may appear farinose after the soredia are shed; summits of the main axes all broken off, those of slender branches densely coralloid, branched.

A fragment of another plant in the collection is fertile; the vegetative portion is identical with that of the sterile plant. Apothecia sessile on slender branches, 3 mm. in diameter, cupulate; exciple densely ramulose with short conical ramuli, appearing subfoveolate between them; marginal cilia erect, very dense, in two rows, less than 1 mm. long, resembling small ramuli; disc concave, flesh color, densely white-pruinose.

In *Gossweiler 9991*, the summits are nearly intact, tapering to acute tips, not coralloid.

ANGOLA: Cuanza Sul, Amboin near Carloaongo-Cuvo River, 1000 m., on dead trees, *J. Gossweiler 9991*, at Kew.

SOUTHERN RHODESIA: Mazoe District, 1320 m., on dead wood, *Frederick Eyles 419*, at Kew.

72. USNEA LYNGEI Motyka, Lich. Gen. Usnea Stud. Monog. 411. 1937.

Type: St. Helena, near tomb of Napoleon, collector unknown, at Oslo.

Thallus pendent, rather flaccid, about 20 cm. long, pale ashy (main axes olive brown below, upper portions and ramuli deep olive buff in our plants); base about

10 mm. long, 0.9 mm. in diameter, lower part black, closely and regularly annularly cracked; closely dichotomous at nearly right angles just above the base, then dichotomous at acute angles with relatively short internodes throughout, minutely tuberculate throughout, each white tubercle bearing a few isidia; ramuli somewhat irregularly disposed, variable in length up to 30 mm. long, flexuous, slender, annularly cracked, not tuberculate or very minutely so at the base of the longer ramuli, tips acuminate but mostly broken off.

A single apothecial initial seen, lateral at the base of a large ramulus, but heavily infected by a parasite before the initial reached 1 mm. in diameter. *Warnecke 107* is too fragmentary for certain determination.

TOGO: *Warnecke 107*, in E. African Herb.
FERNANDO PO: [Santa Isabel Peak], 2900 m., *Gustavo Mann 682 p. p. min.*, at Kew.
ST. HELENA: without locality, *J. D. Hooker*, in Taylor herb. at Farlow Herb.

73. USNEA GOSSWEILERI Dodge, Ann. Mo. Bot. Gard. 43:395. 1956.

Type: Angola, Cuanza Sul, Amboim, Capir near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991*, at Kew.

Thallus erect, fruticose, 5–6 cm. tall, between deep olive buff and tea green; holdfast about 4 mm. in diameter, 2 mm. thick; polychotomous at the top of the holdfast into 7–8 branches about 1.5 mm. in diameter, again densely branched 7–10 mm. above, then rarely branched sympodially in the mid-portion, branches about 1 mm. in diameter, dichotomously branched above, thinning at each dichotomy, annularly cracked but not inflated; surface closely verrucose-tuberculate, forming isidiose soredia, appearing spinulose where the tubercles are crowded and finally farinose after the isidia are shed; ramuli 2–3 (–5) mm. long, irregularly dense, the shorter smooth, the longer minutely tuberculate with acute, often blackened tips; sterile summits short, relatively thick, but tips acute.

Apothecia rare, sessile on the main axes some distance below the summits, or subterminal, 3 mm. in diameter (perhaps immature); exciple smooth; marginal cilia subdistant, annularly cracked at the base, 1–2 mm. long, conic, the longer sometimes dichotomous and minutely tuberculate; disc carneous, white-pruinose.

Cortex 85–100 μ thick, fastigiate, highly gelified, hyphal lumina subdistant within, repeatedly dichotomous in the outer 30 μ where the gel is more deeply stained but without crystals; algal layer 40–60 μ thick, of discrete colonies of *Trebouxia*, about 25 μ in diameter, cells 5–6 μ in diameter, sometimes scattered, sometimes aggregated into a nearly continuous layer; medulla about 160 μ thick, of thick-walled hyphae about 3 μ in diameter, very densely interwoven and heavily nubilated with hyaline or slightly brownish crystals, very lax in the inner 25 μ; axis 230 μ in diameter, of thick-walled longitudinal hyphae, conglutinate in the outer portion, less compact toward the center, with longitudinal air spaces up to 10 μ in diameter between the strands of hyphae.

ANGOLA: Cuanza Sul, Amboim, Capir near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991*, at Kew.

74. Usnea torrida Motyka, Lich. Gen. Usnea Stud. Monog. 327. 1937.

Type: Congo, without locality or collector, in British Museum.

Thallus about 5 cm. tall, erect, rather rigid, citrine drab; holdfast penetrating cracks of bark on twigs; base up to 5 mm. long, about 1 mm. in diameter, scarcely blackened; branching once to thrice dichotomous at the base, occasionally so above; branches variously curved upward, slightly constricted at the base, soon about 1 mm. in diameter, tapering upward; surface smooth between the very dense ramuli; ramuli 0.5–2 mm. long, tips acute, straight or slightly curved upward, occasionally growing out to 5 mm. long as small lateral branches, again sparingly ramulose; on the lower portion the ramuli break off so that the lower internodes appear tuberculate to papillate.

Apothecia terminal, up to 3 mm. in diameter, cupulate becoming nearly plane; exciple closely small-ramulose (not as densely as on the branches); marginal cilia dense, 3–4 mm. long, annularly cracked and bearing a few ramuli; disc concave, flesh color, densely white-pruinose.

The Nyasaland plant is a fragment, less densely ramulose but it agrees otherwise.

Kenya: Northern Frontier Province, summit of Ajao hill, 1030 m., near Buna, on bushes, *I. R. Dale L71 p. p.*, at Kew.

Angola: Northeastern Lunda, Chitato, Dundo near Rio Luachima, 750 m. (Expl. Companhia de Diamantes de Angola), on tall trees, *J. Gossweiler 13928*; Benguella, country of the Ganguellas and Ambuellas, *J. Gossweiler*; both at Kew.

Nyasaland: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., *L. J. Brass 16846* (Vernay Nyasaland Exp. 1946), in N. Y. Bot. Gard. Herb., a fragment tangled with *U. Vainioana* Zahlbr.

75. Usnea picta (Steiner) Motyka, Lich. Gen. Usnea Stud. Monog. 325. 1937. *Usnea ceratina* v. *picta* Steiner, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 106:1:210. 1897.

Type: Kenya, Machakos, corticole, *Liechtenstein*.

Thallus fruticose, rigid, ashy green, 8–10 cm. tall, base very rigid, several times subsympodially branched above the base, axils nearly right angles; branches irregularly divergent, up to 2 mm. in diameter throughout most of the length, tapering gradually to short, branched summits, nearly straight, slightly constricted at the bases, with verruciform papillae, obtuse, denser in the upper portion of the branches; ramuli rather thick, rigid, aculeiform, perpendicular to the branches, tips acute, often branched.

Apothecia abundant, terminal, up to 20 mm. in diameter, nearly plane and densely pruinose when young, becoming convex, often plicate-rugose in the center when old; exciple smooth, glabrous; marginal cilia rather rare, 5–10 mm. long, rigid, conical; disc the same color as the thallus, slightly pruinose; epithecium yellowish; ascospores 6 × 10 μ.

Cortex about 100 μ thick, very hard, chondroid, dilacerate within and perforate in places; medulla about 200 μ thick, dense, K— or yellow next the axis; axis 420 μ in diameter, somewhat effigurate.

I have not seen material certainly referable here. The material Motyka referred to *U. picta* is evidently variable, as three of the six specimens cited are annotated as not typical. *U. isabellina* Dodge from the Northern Frontier Province of Kenya is related to *U. picta*; perhaps the same as the specimen cited by Motyka from southern Usambara, *H. Meyer*, "forma thallo substramineo, haud exacte certa." The Nyasaland plant is closer to Motyka's description but the axes are up to 3.2 mm. in diameter, apothecia only 5 mm. in diameter and the axis 2650 μ in diameter, quite lacerate but not distinctly hollow. I hesitate to describe another new taxon in this group until I have seen more material.

NYASALAND: Zomba Plateau, 1820 m., saxicole, *L. J. Brass 16166* (Vernay Nyasaland Exp.), in N. Y. Bot. Gard. Herb.

76. USNEA ISABELLINA Dodge, Ann. Mo. Bot. Gard. 43:395. 1956.

Type: Kenya, Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L71*, at Kew.

Thallus erect, fruticose, rigid, 7 cm. tall, Isabella color below, shading to chamois above; holdfast 8 mm. in diameter, giving rise to about 10 main axes 1–1.8 mm. in diameter, some branching almost at the base, some up to 20 mm. to the first branch, infrequently dichotomous to subsympodially branched above, terete; cortex smooth, closely annularly cracked and subareolate below, less so above, appearing coarsely papillate from the ramuli breaking off about 0.2 mm. from their bases; ramuli dense, quite fragile, 2–4 mm. long, coarse, slightly verrucose but not becoming sorediate, tips often slightly blackened, some longer ramuli growing out as small lateral branches; ultimate branches up to 40 mm. long, tapering slowly, tips broken off.

Apothecia rather rare, about 5 mm. in diameter, sessile some distance below the tips of the branches, plane to subrevolute; exciple smooth to slightly rugose; marginal cilia fragile, of variable length up to more than 3 mm. long, resembling ramuli; disc avellaneous, slightly white-pruinose.

Cortex 40–50 μ thick, fastigiate, forming a relatively thin-walled pseudoparenchyma, cells 5–6 μ in diameter, the outer 25 μ heavily nubilated with minute brownish crystals; algae *Trebouxia*, in small discrete colonies, some up to 40 μ in diameter, cells 6–8 μ in diameter; medulla 65–80–120 μ thick, of slender (3 μ in diameter) hyphae very densely interwoven and heavily nubilated with minute brownish crystals; axis 500 μ thick, of predominantly longitudinal, thick-walled hyphae about 3 μ in diameter, lumen 1–1.5 μ.

This species seems closest to *U. picta* (Steiner) Motyka, and perhaps the specimen cited by Motyka from Tanganyika, southern Usambara, *H. Meyer* "forma thallo substramineo, haud exacte certa" may belong here. *U. isabellina* differs from

U. picta in color, size, of parts, thinner cortex and medulla and much thicker axis.

KENYA: Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L71*, at Kew.

77. USNEA HORRIDULA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 335. 1937.

Usnea longissima v. *horridula* Müll. Arg., Flora 74:372. 1891.

Type: South Africa, Moorn River near Port Natal (Durban), *Plant*.

Thallus pendent to creeping, up to 30 cm. long, shorter in our plants, olive green drying Mars brown to russet on the main branches, ramuli and tips of branches cinnamon buff, reddish-maculate; base conic, about 2 mm. in diameter, composed of black rooting fibers penetrating the bark, 7 mm. tall, 1.5 mm. in diameter, branching dichotomous at nearly right angles, then curving downwards and flexuous but not parallel, tapering gradually to the short capillaceous summits; cortex cracked and areolate below, verrucose, becoming papillate above the second axil, many papillae growing out to form very dense ramuli about 2 mm. long, annularly cracked at the base, minutely tuberculate, forming soredia, others smoother, up to 7–8 mm. long (perhaps young branches), rather fragile, leaving slightly elevated farinose scars; summits about 10 mm. long, densely dichotomous, slender, tapering to acute tips.

Cortex very variable in thickness in the same section, 80–135 μ, the outer 55 μ of predominantly periclinal branched hyphae, rather closely packed, reddish, the rest more loosely woven, all imbedded in a yellowish gel, paler next the algal layer; algal layer of discrete colonies about 35 μ in diameter, cells *Trebouxia*, about 8 μ in diameter, in some places the colonies quite close, in others distant and dying off; medulla about 210 μ thick, the outer 70 μ pale, of predominantly periclinal hyphae, the rest of very densely woven, very thick-walled hyphae 3 μ in diameter, obscured by brownish crystals; axis 600 μ in diameter, very dense and hyaline with scattered brownish areas about 35 μ in diameter, due to minute brownish crystals which obscure the structure.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.

78. USNEA DALEI Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.

Type: Kenya, Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L70*, at Kew.

Thallus pendent, subrigid, more than 16 cm. long, probably up to 40 cm.; main axes drying deep olive buff, rarely pink-maculate in younger plants and in the more slender distal portions of older plants, the lower portions of the axes of older plants becoming orange cinnamon, the ramuli remaining deep olive buff; holdfast of root-like fibers penetrating the bark, base about 1 mm. in diameter and 2 mm. tall, terete, somewhat blackened and annulate; closely dichotomous to sympodially

branched just above the base, then rarely dichotomous with long internodes throughout; main axes about 1 mm. in diameter, tapering gradually to the tips, acutely few-angled from concrescent rows of papilliform tubercles and the complanate bases of the ramuli, sulcate between the ridges, with a few scattered papilliform tubercles in the furrows; the tubercles growing out as coarse spinules serving as isidia; quite closely ramulose throughout along the acute corticate ridges, mostly about 4 mm. long, nearly cylindric, smooth with rather obtuse tips, a few up to 15 mm. long, curved or flexuous, closely tuberculate with relatively large tubercles in the lower portion, each bearing a few spinules; summits broken off, but such fragments as are present suggest that they are slender, unbranched and not capillaceous.

Cortex 50–55 μ thick, fastigiate, of thick-walled gelified hyphae, the outer 20 μ very deeply staining; algal layer 40 μ thick, a continuous layer of protococcoid cells 8 μ in diameter; medulla 250 μ thick, of thick-walled hyphae 3 μ in diameter, very densely woven next the algal layer and the axis, very loosely woven between; axis 550 μ in diameter, nearly circular in cross-section, the outer 40–50 μ of longitudinal, conglutinate thick-walled hyphae, the rest with single coarse brown hyphae 8 μ in diameter scattered throughout the sclerenchyma, giving the appearance of a section of a monocotyledonous stem such as that of maize.

U. Dalei suggests *U. decipiens* v. *Rhodesiana* Dodge, which is more angled with farinose soredia and which lacks any suggestion of a reddish color on the older axes. *U. Dalei* is the only sulcate species of the SETULOSAE, RUBIGINEAE, somewhat parallel to *U. chloreoides* (GONIODES), but is quite distinct in color and other characters. None of the species of the sulcate subsections, GONIODES nor SULCATAE, bear tubercles in the furrows, nor develop a reddish color.

KENYA: Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L70*, at Kew.

79. USNEA ERUBESCENS (Stein) Motyka, Lich. Gen. Usnea Stud. Monog. 333. 1937.

Usnea articulata f. *erubescens* Stein in H. Meyer, Ostafrikanische Gletscherfahrten, p. 314. 1890; [tr. E. H. S. Calder] Across East African Glaciers, 353. 1891 (with very brief description); Müll. Arg., Flora 73:336. 1890, *nom. nud.*

Usnea barbata v. *articulata* f. *erubescens* Stein, Jahresber. Schles. Ges. Vaterl. Kultur 66:134. 1888, *nom. nud.*

Type: Tanganyika, Kilimanjaro, at tree-line, 3000 m., *H. Meyer*, in Mus. Bot. Univ. Breslau.

Thallus pendent or possibly prostrate, about 20 cm. long, flaccid, drying reddish fuscidulous, dull; base not seen, sparingly dichotomously branched, one branch usually better-developed than the other; branches irregularly curved, up to 2 mm. in diameter; articulate, joints about 1 cm. long, inflated, constricted at the ends,

alternating with short cylindrical joints 0.3 mm. long, some of the larger joints deformed, rugulose and foveolate, almost epapillate, with minute tubercles along the ridges, other large joints smooth; ramuli absent; summits closely branched. Apothecia and soredia not seen.

Cortex about 30 μ thick, soft, fuscidulous; medulla up to 400 μ thick, very lax, white, K—, of irregularly woven hyphae; axis 120–150 μ in diameter, irregular in cross section.

Besides the specimen upon which Motyka based his description, Hans Meyer collected another among mosses of the grasslands at 4000 m., "mit gelbrothen Lager . . . " evidently smaller as he refers to the specimen from 3000 m. as "in sehr kräftigen langbärtigen Exemplaren." *Thomas 619* from Mt. Elgon, 4420 m., may be this entity. It is 5–8 cm. long, ochraceous tawny to ochraceous buff, alternation of long and short joints present but somewhat irregularly so, summits (upper centimeter) rather abruptly more slender, not articulate, slightly tuberculate but not sorediose and chamois to colonial buff. Only more material can show whether our plants are ecologic variants from higher altitudes or whether they represent a distinct taxon. Our plants somewhat resemble the more rigid *U. terricola* Dodge from Cameroons, which shows conspicuous soredia when much younger and comes from a lower altitude. If our reference of the Uganda material is correct and from Motyka's description, *U. erubescens* Motyka is much more closely related to the ARTICULATAE or the AMOENAE, in spite of its reddish color, than to the SETULOSAE, RUBIGINEAE, where Motyka places it.

UGANDA: Mt. Elgon, Masaba, 4420 m., on rocks in alpine meadow, *A. S. Thomas 619*, at Kew.

80. USNEA SUBFLORIDA (Zahlbr.) Motyka, Lich. Gen. Usnea Stud. Monog. 335. 1937.

Usnea Steineri v. *subflorida* Zahlbr., Bot. Jahrb. [Engler] 60:541. 1926.

Type: Tanganyika, Meru District, *Fassmann*.

Thallus erect, rigid, fruticose, 4–5 cm. tall, roods brown to pecan brown to wood brown and avellaneous in South African specimens (under 12× magnification irregularly light yellowish olive with coral red spots, reddish fuscous spotted with greenish fuscous, *fide* Motyka); holdfast 3 mm. in diameter, hemispheric, of coarse, branched rootlets, nearly black, base about 1 mm. in diameter below expanding to 1.5 mm. at the first dichotomy, about 5 mm. tall; thrice dichotomous with short internodes just above the base, axes about once dichotomous above; branches straight or curved, about 1.5 mm. in diameter below, tapering to 1 mm. below the apothecia; articulate, joints long, inflated below and tapering above, constricted at the ends, terete, papillose, some papillae forming spinules which break off as isidia; ramuli rather dense, 3–5 mm. long, the longer slightly tuberculate, tips acuminate but mostly breaking off, leaving an obtuse end as the cortex regenerates.

Apothecia up to 6 mm. in diameter, subterminal but appearing terminal when they mature, the branch often passing within the exciple and the tip emerging as a stouter cilium, cupulate to nearly plane; exciple with branched radial ridges becoming subfoveate, slightly tuberculate along the ridges; marginal cilia moderately close to subdistant, up to 4 mm. long, radiating, straight or flexuous, annularly cracked at the base, tapering to acute tips, maculate, the larger tuberculate; disc densely white pruinose when young, becoming dark flesh color in age.

KENYA: Mau forest, Endabarra, 2355 m., on trees at edge of *Acacia* grove forest, *P. R. O. Bally B4947 p. p. min.*, at Kew.

CONGO: Mt. Kahusi, 2700 m., ramulicole, *F. L. Hendrickx 4300*, small and moribund, in E. African Herb.

SOUTH AFRICA: Transvaal, Zoutpansberg district, near "Punch Bowl" Inn, on decaying tree trunks, *O. Almborn*, Lich. Afric. 19, in Dodge Herb.

81. USNEA BICOLORATA Motyka, Lich. Gen. Usnea Stud. Monog. 336. 1937.

Type: Congo, Eastern Province, Kivu Mts., *de Witte*.

Thallus subpendent, 12 cm. long, rigid, pale ashy olive green, irregularly red-spotted; base quite slender, rigid, blackened, slightly attenuate, infrequently sympodially branched almost to the summits, axils 90° or nearly so; branches up to 2 mm. in diameter, rather uneven in thickness, slightly attenuate at the base, abruptly so at the summits, irregularly curved, rarely deeply cracked; more or less terete, indistinctly deformed, and slightly foveolate, papillae obtuse, concolorous, tubercles forming soralia in the upper portion of the thallus, soralia relatively broad, white-farinose, becoming eroded; ramuli quite close, of variable length, similar to branches from dichotomies; summits indistinct, dense. Apothecia not seen.

Our plants from Cameroons are tangled with *Usnea speciosa* and *U. hispida*. They are nearly all Vandyke brown to Natal brown on the main axes although under 12× mignification small patches of citrine drab and dark olive buff are visible and the broken cortex is red-maculate; the medulla is as thick as the axis; otherwise they agree with the above description translated from Motyka. In *Bally B4947*, the soralia are apotheciiform, up to 0.5 mm. in diameter, wider than the branches which bear them.

CAMEROONS: Victoria, in Meyer Crater, 2580 m., on *Aquaria salicifolia*, *T. D. M. 917 p. p. min.*, ex hb. Bot. Gard. Victoria, at Kew.

KENYA: Mau forest, Endabarrá, 2355 m., on trees at edge of *Acacia* grove forest, *P. R. O. Bally B4947*, glued to sheet of *U. aequatoriana* Motyka, at Kew.

82. USNEA SPILOTOIDES Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.

Type: Kenya, Chyulu hills, *H. D. van Someren*, in East African Herb.

Thallus probably procumbent, perhaps pendent, subrigid, about 10 cm. long, russet below, shading through tawny to zinc orange and ochraceous salmon, with smaller ramuli pale olive buff; base not seen; branching sympodial or very closely

dichotomous in basal portion where axes are up to 0.9 mm. in diameter, tapering to short subcapillaceous summits, irregularly dichotomous above, some internodes long, others quite short, axils nearly 90°; branches very flexuous, summits mostly recurved, articulate, joints slightly inflated, ends constricted, very variable in length, rarely the cortex regenerating to form very short, darker joints up to 0.3 mm. long, but usually joints separated by a narrow crack; minutely white verrucose, producing single or very few isidia; ramuli very irregularly disposed, sometimes very close, 4 (–10) mm. long, very fragile, slightly verrucose, producing isidiose soredia, becoming minutely farinose as the soredia are shed; ramuli on more slender branches subdistant, about 1 mm. long, smooth, tips acute with long nude areas; summits mostly broken off, up to 20 mm. long, slender, tips acuminate, some nude, others very sparsely short ramulose.

Cortex 55–80 μ thick, of yellow conglutinate thick-walled radial hyphae 7–8 μ in diameter, lumen 1 μ; algal layer 40 μ thick, of protococcoid cells up to 12 μ in diameter, dying in places; medulla 75 μ thick, the outer 35 μ of predominantly periclinal, thick-walled hyphae 5–6 μ in diameter, lumen 3 μ, forming a pseudoparenchyma, the inner 40 μ of slender, densely woven thick-walled hyphae, heavily nubilated with minute brown crystals; axis 650 μ in diameter, solid, of longitudinal, conglutinate thick-walled hyphae 4–5 μ in diameter, lumen 3 μ.

This species belongs in the group with *U. erubescens* and *U. spilota.* Perhaps some of the material referred by Motyka to the latter species may belong here, as Motyka states that the collections from South Africa are "minus certa" and one "juvenilia, possibile ad *U. horridulam* non evolutam spectantia." *U. horridula* differs from *U. spilotoides* in its non-articulate, more regularly ramulose thallus with the isidiose soredia confined to upper parts of the ramuli.

KENYA: Chyulu hills, *H. D. van Someren,* in E. African Herb.

83. USNEA MEYERI (Stein) Motyka, Lich. Gen. Usnea Stud. Monog. 338. 1937. *Usnea cornuta* v. *Meyeri* Stein, Jahresber. Schles. Ges. Vaterl. Cultur 66:134. 1888.

Type: Tanganyika, Kilimanjaro, 4000 m., saxicole, *H. Meyer.*

Thallus 4–6 cm. tall, erect, very rigid, greenish-stramineous, reddish-maculate, main axes becoming Van Dyke brown, slender branches and ramuli clay color to cinnamon buff, summits nearly white from soredia in the herbarium; holdfasts of radiating, closely branched rootlets, spreading over the surface of the rock and penetrating between the crystals; base about 10 mm. tall, 2 mm. in diameter, cortex annularly cracked and areolate; about thrice dichotomous with very short internodes (appearing polychotomous), each axis with a long internode (10 mm. or more) then again densely branched, the branches terete, curving upward to form a depressed hemispheric tuft; the lowest internode about 2 mm. in diameter, thinning at each dichotomy, the ultimate branches still about 1 mm. in diameter; the lower two internodes blackened, the upper branches clay color to cinnamon buff, testa-

ceous-maculate; surface smooth or low-tuberculate, forming soralia of black-tipped isidiose soredia becoming confluent on some of the ultimate branches; ramuli very irregularly distributed, absent on some branches, subdistant on others, about 2 mm. long, annularly cracked at the base, slightly inflated, tapering to an obtuse tip, some up to 5 mm. long, slightly tuberculate and occasionally forked (perhaps young secondary branches). Apothecia not seen.

Cortex 100 μ thick, so blackened that structure is not clear; algal layer about 60 μ thick in discrete colonies of *Trebouxia* (mostly disintegrated, leaving regularly spaced lacunae just under the cortex, with an occasional cell or small colony remaining; medulla about 160 μ thick, of mostly periclinal thick-walled hyphae about 3 μ in diameter, axis 1000 μ in diameter, solid, of longitudinal conglutinate hyphae interlaced with strands of transverse hyphae.

KENYA: west slope of Mt. Kenya, on trail from West Kenya Forest Station to summit, 3630 m., in giant heath zone, *Edgar A. Mearns 1521, 1536* (T. Roosevelt Exp.), at Farlow Herb.

83a. Var. CHONDROCLADA (Steiner) Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.
Usnea chondroclada Steiner, Verhandl. Zool. Bot. Ges. Wien 53:228. 1903.

Type: Cameroons, Fako, 3600–3800 m., on lava blocks, *Alfred Bornmueller.*

Thallus 4–6 cm. tall, erect, rigid, axes Sayal brown shading to light brownish olive, ramuli Isabella color, indistinctly reddish-maculate; holdfast broken off, base black, 5 mm. tall, 1 mm. in diameter below, expanding to 2 mm. just below the first dichotomy; repeatedly dichotomous just above the base, then sparingly so above; branches 1.3–1.5 mm. in diameter, annularly cracked, not inflated below, slightly so above, thinning somewhat at each dichotomy, slightly verruculose, some verrucae growing out as small ramuli; secondary branches slender, up to 0.6 mm. in diameter, paler and some more clearly reddish-maculate; ramuli from less than 1 mm. to 5 mm. long, slightly inflated, tips acuminate, blackened; the smaller ramuli easily break off leaving minute white scars and probably serve as isidia, especially in the upper portions of the smaller secondary branches and the obtuse summits. Apothecia not seen.

Cortex 65 μ thick, fastigiate, gelified, outer 15–30 μ dark brown, algal layer about 30 μ thick, of *Trebouxia,* cells 7–8 μ in diameter; medulla 100 μ thick, densely woven under the algal layer, looser next the axis, hyphae 3 μ in diameter, lumen about 1 μ; axis solid, about 300 μ thick, of longitudinal conglutinate hyphae interlaced with strands of transverse hyphae.

CAMEROONS: Cameroon Mt., *Alfred Bornmueller* sub *U. chondroclada* f. *ramillosa* Steiner, herb. nom. ? com. Zahlbruckner, in Howe herb. at Farlow Herb.

84. USNEA MACULATA Stirton, Scottish Nat. 6:293. 1882.
Usnea Flotowii v. *subhispida* Zahlbr., Bot. Jahrb. [Engler] 6:541. 1926.

Type: S. Africa, Cape of Good Hope, Somerset East, *P. MacOwan & J. M'Lea,* in Art Galleries of the Glasgow Corporation.

Thallus erect, fruticose, up to 7 cm. tall, pale greenish drying pecan brown to vinaceous tawny (under low magnification spotted with deep olive buff); holdfast a black disc up to 10 mm. in diameter, composed of closely woven rooting fibers giving rise to erect axes, mostly unbranched below, some dichotomous just above the holdfast, blackened for 2–5 mm. at the base, sparingly unequally dichotomous in the upper portion; axes forming a dense erect tuft 10–40 mm. in diameter; subarticulate, joints relatively long and slightly constricted at the ends, up to 1.6 mm. in diameter a short distance above the base, more slender above; surface rather closely tuberculate to subpapillate, papillae either single or concrescent in short irregular ridges, some growing out as caducous, conical spinules about 0.5 mm. long, a few growing out as fragile ramuli, 5–10 mm. long, the larger annularly cracked with obtuse tips, curved, ascending; scars from fallen spinules and smaller ramuli resembling small farinose soralia.

Apothecia sessile on smaller branches, 3–4 mm. in diameter, cupulate; exciple citrine drab to deep olive buff, smooth to slightly tuberculate near the base; marginal cilia dense, up to 5 mm. long, coarse, annularly cracked, slightly constricted at the base, tips obtuse, many broken off; disc concave, somewhat deformed, coarsely cream buff-pruinose.

The apothecia of our plants are apparently young and agree with those described by Motyka for *U. subflorida* (Zahlbr.) Motyka except those of the latter are terminal instead of lateral. The vegetative portion of the plants agrees with that of *U. maculata*. Perhaps when a fuller series of specimens is available, it will be necessary to unite *U. subflorida* with *U. maculata*. Some of our plants are from farther north than either species has been reported. *Greenway 6532* is very young, about 1 cm. tall and sterile, but probably should be referred here.

SUDAN: Mt. Kinelli, 3360 m., on pole and cairn, *T. F. Chipp 64*, at Kew.
UGANDA: Ruizi River, 1390 m., on trees in riverine forest, *T. Jarrett 402 p. p.*, at Kew.
TANGANYIKA: S. Pare Mts., Mt. Mtonto, 2100 m., ramulicole, *P. J. Greenway 6532*, at Kew.
SOUTH AFRICA: without locality, *Drège*, ex herb. W. Sonder sub *U. fragilis* Laurer, herb. nom.?, in Tuckerman herb. at Farlow Herb.
MADAGASCAR: Imerina, Andrangoloaka, *Hildebrandt 2173*, Nov. 1880, com. C. Rensch ex herb. Sbarbaro sub *U. barbata* v. *scabrosa* (Ach.) Müll. Arg., at Farlow Herb.

85. USNEA ACANTHERA Vainio in Motyka, Lich. Gen. Usnea Stud. Monog. 358. 1937.

Type: S. Africa, Bechuanaland, Crocodile River, *Klingsberg*, in Riksmuseet, Stockholm.

Thallus prostrate to suberect, rigid, about 6 cm. long, ashy green, darker on the main axes; divaricately dichotomous just above the base and sparingly so below the summits; axes 1 mm. in diameter, sigmoid-curved, continuous, terete, surface uneven, not papillate although very young ramuli may simulate papillae; ramuli dense, strigose, perpendicular, about 2 mm. long, pale green, smooth.

Apothecia terminal, up to 7 mm. in diameter, almost plane; exciple slightly uneven or rugose, densely ciliate; marginal cilia dense, 4–5 mm. long; disc subplane, margin often broken, flesh color, almost epruinose; epithecium fusco-fuligineous; ascospores 6 × 9 μ in narrow asci.

Cortex 30 μ thick, chondroid, pale green; medulla 120–140 μ thick, rose color, dense, K—; axis 360 μ in diameter, white with narrow central cavity, slightly spotted with a few black hyphae.

Our specimens seem to be juvenile forms of this species. The branching is dense at the woody base, 4 mm. in diameter, 5 mm. tall, only once dichotomous above in about the middle of the axis, branches nearly straight; ramuli 3–5 mm. long; summits slender, the uppermost 10 mm. eramulose. Sterile but not sorediose in the Kenya specimen, a few very young apothecia present in the Uganda specimen.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.
UGANDA: Kigezi, Mafuga, 2410 m., *I. R. Dale L41 p. p. min.*, at Kew.

86. USNEA MAROCANA Motyka, Lich. Gen. Usnea Stud. Monog. 359. 1937.

Type: Maroc, Camp Monod, arboricole, *Mouret*.

Thallus 5–8 cm. tall, fruticose, pale ashy green, drying deep olive buff to olive buff; dichotomous just above the holdfast and twice or thrice dichotomous below with rather short internodes and once or twice dichotomous at the summits; nearly terete with occasional low ridges where the ramuli are close in rows; branches mostly 1.2–1.3 mm. in diameter in the lower three fourths of their length, then tapering upward to slender acute summits; surface smooth except for young ramuli or isidia; ramuli rather close, tending to form vertical rows, bases of the larger ramuli somewhat complanate, the smaller less so; mostly 5–10 (–15) mm. long, often annularly cracked just above the base, slightly inflated in the middle and tapering to acute tips, mostly smooth below, verrucose and isidiose above, the verrucae appearing minutely farinose after the isidia are shed.

Cortex 65–90 μ thick, probably fastigiate but so gelified as to appear structureless; algal layer continuous, 30–40 μ thick, of *Trebouxia*, cells 5–6 μ in diameter, with some colonies invading to the middle of the cortex; medulla pinkish, compact, about 130 μ thick, of thick-walled interwoven hyphae; axis about 1100 μ in diameter, appearing solid, but lacerate with scattered small cavities about 10 μ in diameter.

SIERRA LEONE: Gebense, Sefadu, on trunk of *Elaeis guineensis*, *F. Adames*, com. *F. C. Deighton M4756*, at Kew.

87. USNEA AMPLISSIMA Stirton, Scottish Nat. 6:106. 1881.

Usnea arthroclada subsp. *arthrocladodes* Vainio, Cat. Welwitsch's African Pl. 2:397. 1901.

Type: S. Africa, Cape of Good Hope, Somerset East, *P. MacOwan*. Type of *U. arthroclada* subsp. *arthrocladodes* Vainio is: Angola, Golungo Alto, Serra do Alto Queto, *Welwitsch 69 p. p.*; both in British Mus.

Thallus about 60 cm. long, pendent, very rigid, ashy or pure green, partly paler and very slightly reddish; base very large and firm, infrequently but several times dichotomous, axils 90°, branches arcuate, pendent, of nearly the same diameter throughout, up to 2.5 mm. in diameter, tapering slightly at the ends, neither exactly terete nor clearly angled; surface uneven, irregularly subareolate, closely annularly cracked, the cortex regenerating at the cracks, paler or pinkish, wherefore the surface appears irregularly rugose and scabrous on account of the areolation and the coarse concolorous tubercles; ramuli close, slightly curved, very thick at the base, tapering gradually to the tips, the thicker ones tuberculate and sometimes branched, the more slender ones smooth, tips obtuse, closely annularly cracked and subulate.

Apothecia abundant, usually at the tip of a lateral branch, 10–20 (–30) mm. in diameter, nearly plane; exciple smooth (subfoveolate on very large apothecia); marginal cilia not dense, radiating, about as long as the diameter of the disc, usually not branched, annularly cracked, tips acuminate, usually smooth but some of the longer ones slightly tuberculate; disc plane or slightly rugose in the larger apothecia, dirty flesh color, slightly pruinose; thecium about 70 μ tall, epithecium greenish fuliginous, ascospores 11 $\times$ 7 μ in slightly inflated asci.

Cortex about 100 μ thick, chondroid, but soft, fragile, green with reddish spots; medulla about 180 μ thick, white, dense, K—; axis about 500 μ thick, white.

The above description is translated from Motyka as our specimens are rather young, only about 15 cm. long and sterile. The cortex is areolate but not slightly rugose. Since no suggestions of soredia on the tubercles have been seen, it is possible that our material may be young *U. distensa*; however, in our younger plants of that species, about the size of the present plants, soredia have already developed. The specimen from Kenya is only a fragment from the middle of the thallus but it is abundantly fertile.

KENYA: western slope of Mt. Kenya along trail from West Kenya Forest Station to summit, 3630 m., in giant heath zone, *Edgar A. Mearns 1533* (T. Roosevelt Exp.) ex G. K. Merrill herb., at Farlow Herb.

ANGOLA: Cuanza Sul, Amboim, Capir near the Carloaongo-Cuvo River, 1000 m., *J. Gossweiler 9991*, at Kew.

88. USNEA DISTENSA Stirton, Scottish Nat. 6:104. 1882.

Type: S. Africa, Cape of Good Hope, Griqualand West, Kimberley Diamond Fields, *T. Shaw*, in Art Galleries of the Glasgow Corporation.

Thallus pendent, rigid, up to 70 cm. long (only 15 cm. in the type), green, drying deep olive buff; holdfast up to 8 mm. in diameter, blackened, base 2 mm. in diameter, about 10 mm. long, closely annulate, blackened for a variable distance in different plants, then closely dichotomous above the base (axils 90°) and less frequently and more irregularly so above; main axes about 1.5 mm. in diameter, thinning at each dichotomy to the capillaceous tips (about 6–10 cm. long), closely

annulate and subareolate on the main axes, smooth with a few minute pale tubercles, becoming more and larger tuberculate on the more slender branches, sometimes somewhat foveolate and angled; sparingly and irregularly ramulose on some main axes, quite closely so on others; ramuli about 25 mm. long, closely tuberculate, forming soralia of isidiose soredia, the more slender branches more regularly and closely ramulose, the ramuli shorter, 5–15 mm. long, more slender and less tuberculate, all ramuli rather fragile. Apothecia not seen.

Our Central African material is rather short, mostly about 30 cm. long, and may represent young plants although abundantly sorediiferous. The main axes are not subscrobiculate from regenerating cortex of the fissures; otherwise it agrees well with Motyka's description.

UGANDA: Mt. Elgon, 1290 m., on trees, *W. Small 218* (fragments from terminal portions of the thallus).

TANGANYIKA: Usambara, Amani, 1000 m., in rain forest, *P. J. Greenway 998*, in E. African Herb. and at Kew; Amani-Maramba, 1030 m., *P. J. Greenway 4151*, in E. African Herb.

SOUTH AFRICA: Cape of Good Hope, Griqualand West, Kimberley Diamond Fields, *T. Shaw*, in Art Galleries of the Glasgow Corp.; Cape of Good Hope, Knysna, on *Quercus*, *O. Almborn*, Lich. Afric. 18, in Dodge Herb.

CONGO: km. 30, route Kahusi, *F. L. Hendrickx 4330*, in E. African Herb.
18, in Dodge Herb.

MAURITIUS: without locality or collector, ex herb. Macreight in Tuckerman herb. sub *U. plicata*, at Farlow Herb.

89. USNEA PROMONTORII Motyka, Lich. Gen. Usnea Stud. Monog. 386. 1937.

Type: S. Africa, Cape of Good Hope, in primeval forest, *Rehman*.

Thallus pendent, quite rigid, more than 100 cm. long, pale ashy green (Motyka) drying chamois to cream buff in our material; base not seen; branching dichotomous, axils usually 90°, complanate, the branches curving downward until the axes are nearly parallel, internodes very long, subflexuous to straight, the ultimate 20 cm. unbranched, about 1 mm. in diameter below, tapering to the long slender tips; cortex of main axis coarsely areolate, margins of areoles slightly elevated, giving a rough, subrugose appearance, the more slender portions with scattered low, pale tubercles, often in somewhat oblique rows, perhaps giving rise to small soralia but not present in our South African material (a few in our Kenya specimens); ramuli irregularly disposed, sometimes quite close, in other places subdistant, fragile, 5–15 (–20) mm. long, curved, axils not complanate, slender, tapering to acuminate tips.

Except for greater length and color, our plants agree closely with Motyka's description.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4316*, basal fragment only, in E. African Herb.

KENYA: Mau forest, Endabarra, 2030 m., in *Acacia* shrub forest, *P. R. O. Bally B4947*, in E. African Herb.

SOUTH AFRICA: Cape of Good Hope, Knysna District, Hermansdorp Division, on

branches of *Podocarpus Thunbergii*, *A. W. Woodcock*, ex hb. Mus. Austro-Africanum, at Kew.

MAURITIUS: without locality, *Sieber 43*, in Tuckerman herb. sub *U. plicata*, at Farlow Herb.

90. USNEA GONIODES Stirton, Scottish Nat. 6:108. 1881.

Usnea angulata f. *goniodes* Hue, Nouv. Arch. Mus. Paris, IV. 1:45. 1899, *quoad nomen sed non descriptio.*

Type: South Africa, Cape of Good Hope, *H. Bolus 517*, in Art Galleries of the Glasgow Corporation. Hue based his new combination on a plant from Paraguay, Peribebuy, *Balansa 4140*, probably *U. sulcata* v. *neutra* Motyka, from his description.

Thallus pendent, subrigid, about 30 cm. long, green, drying deep olive buff (finally sayal brown to snuff brown in the type); holdfast a dark disc about 2 mm. in diameter, on the upper side of a twig from which two or more axes arise, 0.5–0.7 mm. in diameter, about 2 cm. long, cylindric, annulate with very few ramuli, curving over either side of the twig, then dichotomous and becoming triangular in cross-section; cortex irregularly annular and subareolate, ridges usually corticate, sometimes cracked, up to 1.2 mm. in diameter (only 0.8 mm. in our rather young material), very rarely dichotomous above; axes flexuous and subparallel throughout, thinning gradually to the very slender, almost cylindric filiform summits; ramuli from the ridges, bases complanate, quite close, mostly about 10 mm. long, very slender, an occasional one growing out as a very slender lateral branch up to 50 mm. long, with small ramuli, the larger ramuli tuberculate and sometimes isidiose sorediose.

Apothecia up to 15 mm. in diameter, at the tips of lateral branches, plane; exciple slightly to deeply rugose-reticulate and sublacunose, epapillate; marginal cilia few and often missing, up to 10 mm. long, tuberculate; disc plane, distinctly rugose, flesh color, chalky, pruinose (olive buff in type and in *Brass 16992*).

Cortex 55–65 μ thick, fastigiate, of very thick-walled, conglutinate hyphae, the outer 20 μ slightly brownish; algal layer 25 μ thick, of closely packed cells of *Trebouxia* 6–8 μ in diameter; medulla about 130 μ thick, of densely woven thick-walled hyphae, heavily nubilated with dark brown minute crystals, more loosely woven about 40 μ outside the axis and tearing on sectioning; axis 730 μ thick, appearing solid but minutely lacerate with many small cavities about 10 μ in diameter in the inner three fourths of the axis, of thick-walled hyphae 6–8 μ in diameter, lumen 3 μ.

Some of our material is young and sterile. In several places, some injury to the cortex has been followed by a dense branched tuft of ramuli. *Gossweiler 13654* consists of a few fragments as if broken from the middle of the primary axes, or perhaps younger plants; *Brass 16992* is a fragment from the terminal portion of the thallus, fertile, quite typical except that the soredia are less developed than in the type.

ANGOLA: nordeste de Lunda, Dundo near Rio Luachimo, 700 m., *J. Gossweiler 13654*.
NYASALAND: Mt. Nchisi, corticole, *L. J. Brass 16992* (Vernay Nyasaland Exp., 1946), in N. Y. Bot. Gard. Herb.
PORTUGESE EAST AFRICA: without locality, *J. Stocks 39*; Mozambique, Inhambane, on *Copaifera*, without collector, a fragment separated from material of *U. trichodoides* Vainio; both at Kew.
SOUTH AFRICA: Cape of Good Hope, *H. Bolus 517*, type in Art Galleries of the Glasgow Corporation; Adelaide, *Miss Brugton*, com. Rev. W. Lillie, in Howe herb., det. *U. angulata* by M. Bouly de Lesdain, cited by Motyka (Monog. p. 397), at Farlow Herb.

91. USNEA CHLOREOIDES (Vainio) Motyka, Lich. Gen. Usnea Stud. Monog. 397. 1937.

Usnea angulata f. *chloreoides* Vainio, Hedwigia 37:40. 1898.

Type: Uganda, near Mt. Ruwenzori, Nzowi Nez, 0° 5′ S., *Scott-Elliott*.

Thallus pendent, subrigid, about 50 cm. long, between citrine drab and deep grape green; base not seen; frequently dichotomous, branches somewhat flexuous, quite uniformly 1.2 mm. in diameter, frequently and irregularly transversely cracked, angulate, the ridges formed of coalescent rows of coarse papillae, many of which develop into ramuli, with occasional tubercles between, axis not conspicuously sulcate, some ridges quite high and almost alate; ramuli dense, very fragile, annularly cracked, tuberculate, 3–6 mm. long, tapering upward but tip obtuse and slightly brownish.

Apothecia absent in the type, abundant in our plants, up to 10 mm. in diameter, lateral on short lateral branches about 0.3 mm. in diameter, stalks coarsely papillate, not angled, quite fragile; exciple deeply incised, margin lobed, smooth, nearly plane; marginal cilia few, 1–3 mm. long, conical, quite fragile; disc plane, vinaceous cinnamon, slightly pruinose when young.

Under two of the apothecia, the branch has grown out beyond the apothecium for 7 cm., about 0.5 mm. in diameter. With some hesitation I have referred our fertile coastal lowland material to a sterile species from the highlands of Mt. Ruwenzori. The thallus agrees quite well with Motyka's description, except for more abundant and shorter ramuli and more alate ridges, the upper portion of which often break away, leaving long white scars.

KENYA: Tana River, 16 m., on trees, *E. Battiscombe 227*, at Kew.
PORTUGESE EAST AFRICA: Lourenço Marques, *Cecil P. Cross*, ex herb. G. K. Merrill, at Farlow Herb.
MADAGASCAR: Fort Dauphine, *native collector*, com. F. G. Paris ex herb. H. E. Hasse, at Farlow Herb.

92. USNEA FERNANDIAE Duvigneaud, Bull. Soc. Roy. Bot. Belg. 85:110. 1952.

Type: Congo: Bas-Congo, Ngombe-Matadi, *Paul Duvigneaud 305 U3*, in Herb. Duvigneaud, portion of type in Bot. Mus. Lund., loaned by Dr. Ove Almborn.

Thallus pendent, subrigid, 70 cm. or more long, flexuous, grayish green; primary holdfast not surely seen, but secondary holdfasts formed where lateral branches come in contact with a twig, consisting of discrete, radiating rooting fibers forming a disc 1 mm. in diameter; secondary bases terete, of variable length, cortex smooth, subannularly cracked; irregularly dichotomous at nearly right angles but the branches soon curving downward and subparallel, axils slightly complanate; branches mostly 4- to 5-angled with low obtuse ridges, occasionally acute but not alate, from concrescent rows of tubercles, scars of minute fallen spinules and the complanate bases of ramuli, but in some places almost terete, plane or slightly convex between the ridges, irregularly annularly cracked; slender lateral branches perpendicular to the main axes, terete, 20–40 mm. long, 0.4–0.6 mm. in diameter, sparingly ramulose, minutely tuberculate from scars of fallen spinules, abruptly tapering to acute tips which are sometimes forked; ramuli mostly 5–7 mm. long, about 0.2 mm. in diameter, cortex smooth, rarely annularly cracked above the somewhat complanate base, tips acute but very fragile and mostly broken off; summits more slender and fragile but not very distinct.

Apothecia (absent in specimen available) at tips of slender lateral branches, up to 15 mm. in diameter; exciple smooth; marginal cilia few or none; disc almost plane, white-pruinose.

Cortex 35 μ thick, gelified, fastigiate, outer 6 μ filled with dark brown granules, thinning over the ridges and regenerating in cracks until it reaches the bottom of the algal layer; algal layer about 80 μ thick, of discrete colonies of *Trebouxia* 15–20 μ in diameter, forming a nearly continuous layer on the outside, less close within, cells 6–7 μ in diameter; medulla 80–100 μ thick, densely woven just under the algal layer and next the axis, very lax between, hyphae 3 μ in diameter, lumen less than 1 μ; axis 420 μ in diameter, with two cavities near the center, each about 50 μ in diameter, of longitudinal, thick-walled hyphae 6–7 μ in diameter, lumen nearly 2 μ, with scattered thin-walled hyphae 6–7 μ in diameter, filled with a deep yellow, highly refractive material (oil?), scattered singly or lying side by side in short rows, not radially arranged.

The portion of the axis available for study is younger than that of *U. bakongensis*; perhaps in the older part of the axis, the central cavities coalesce to form a relatively large central cavity as in that species, which it resesmbles in structure of the axis. The medulla is better differentiated and laxer in *U. Fernandiae*.

CONGO: Bas-Congo, Ngombe-Matadi, *Paul Duvigneaud 305 U3*, cotype in Bot. Mus. Lund.

93. USNEA AFRICANA Motyka, Lich. Gen. Usnea Stud. Monog. 398. 1937.

Type: Tanganyika, Usambara Muandara forest, *C. Holst.*

Thallus pendent, subrigid, up to 110 cm. long, dark olive buff, ramuli olive buff (from soredia); base absent in our material, frequently dichotomous just above the base, then occasionally so throughout, branches often more or less twisted about

each other (wind action?), branching at right angles, the two branches curving downward below the axil to become almost parallel, somewhat flexuous, the proximal portion up to 1.8 mm. in diameter, tapering evenly to the summits; cortex irregularly transversely and longitudinally cracked, with a few low longitudinal ridges (more in *Eyles 1023*) formed from the complanate axils of the ramuli; ramuli 4–10 (–20) mm. long, densely verrucose with soralia of isidiose soredia, quite fragile, tips acute. Similar soralia from the verrucae are abundant on the more slender portions of the main axes.

T. W. Maitland 396 is doubtfully referred here. It consists of a coarser, more rigid plant, axis 2 mm. or more in diameter, more conspicuously angled and less frequently dichotomous; the ramuli are 20–30 mm. long and thicker. The Kenya plant is also doubtful. It consists of fragments about 10 cm. long, the main axes tawny olive to clay color, the ramuli chamois to cream buff. It seems closer to *U. africana* than to the STRAMINEAE, SULCATAE.

KENYA: uplands, 2250 m., *E. R. V.*, ex Corydon Mus. 5161, at Kew.
UGANDA: Busoga, Jinja, 1590 m., *E. Brown 91*, ex Bot Gard. Entebbe; Mile 8 on Masaba Road, 1130–1240 m., *F. Chandler 1891*, moribund; Bangala, Sese, 1190 m., *T. W. Maitland 396*; all at Kew.
TANGANYIKA: Mpwampwa, Kiboriani Mt., 1770–1930 m., *B. D. Burtt 3880*; Kondoa District, on *Oxyanthus speciosus* DC., *B. D. Burtt 1183*, at Kew.
S. RHODESIA: Matopos, 1610 m., *Frederick Eyles 1023*; Melsetter District (Gazaland), Chimanimani, 2250 m., *C. F. M. Swynnerton 617*; both at Kew.

94. USNEA BAKONGENSIS Duvigneaud, Bull. Soc. Roy. Bot. Belg. 85:109. 1952.

Type: Congo: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud 582 U2*, in herb. Duvigneaud, portion in Bot. Mus. Lund, loaned by Dr. Ove Almborn.

Thallus pendent, 70 cm. and more long, subrigid, grayish green; primary holdfast broken off in specimen studied, secondary holdfasts fibrous discs 3–4 mm. in diameter, dark brown; secondary base about 1 mm. in diameter, of variable length, cortex annulate and subareolate; main branches 1–1.5 mm. in diameter below, tapering gradually to more closely ramulose, capillaceous summits about 7 cm. long; rather sparingly dichotomous at about 45° angles, the branches slowly curving downward; below nearly terete except for complanate bases of small lateral branches, rather closely annularly cracked, the cracks regenerating as transverse ridges with minute low tubercles producing 1–3 spinules, becoming irregularly angular above from short longitudinal ridges formed by the complanate bases of small lateral branches, or ramuli, and the upturned edges of longitudinal cortical cracks with rows of scars of fallen spinules, closely but incompletely annularly cracked forming transverse ridges as in the lower portion, with scattered scars of fallen spinules between; ridges less conspicuous toward the summits which are terete with rare scars; ramuli mostly broken off below, subdistant, becoming closer above, especially on the capillaceous summits, 5–10 mm. long, the shorter smooth, the longer covered with minute, fragile spinules.

Cortex 65–80 μ thick, gelified, fastigiate, hyphal lumina about 1 μ in diameter, the outer 10 μ heavily nubilated with brown granules; algal layer about 225 μ thick, of discrete colonies of *Trebouxia*, about 25 μ in diameter, forming a nearly continuous layer on the outside with similar colonies less closely packed almost to the axis, the inner 25 μ with only an occasional colony; medulla not differentiated as a distinct layer unless the inner 25 μ of the algal layer be so considered; axis 800 μ in diameter, wall 170–200 μ thick, of longitudinal thick-walled, conglutinate hyphae 3.5 μ in diameter, lumen 1 μ, with thin-walled hyphae 5–6 μ in diameter arranged in nearly continuous, mostly radial rows (suggesting the appearance of rays in transverse sections of coniferous wood), cell contents highly refractive as if filled with an oil or resin, colored deep brownish yellow; central cavity stellate in outline of transverse section, 400–460 μ in diameter, probably formed by the coalescence of 7–8 central cavities, loosely filled with contorted, thick-walled hyphae 6–7 μ in diameter, lumen about 2 μ, nubilated with minute hyaline granules.

In the original description, Duvigneaud states "medulla et axis K lutescentes et dein rubescentes." In the specimen studied, on shaving off the cortex of an upper portion of a main branch and treating with K, a yellow color promptly develops which goes into solution in K, leaving the exposed medulla white when the solution is blotted off. Mounting transverse sections near the base of a main branch in K, all color disappears from the sections except for algal cells.

CONGO: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud 582 U2*, in herb. Duvigneaud, portion of cotype in Bot. Mus. Lund.

95. USNEA LIVIDA Motyka, Lich. Gen. Usnea Stud. Monog. 419. 1937.

Type: Cameroons, Mt. Cameroon, *Winkler*.

Thallus 100 cm. long, pendent, flaccid, uniformly ashy green, partly slightly fuscescent (dark olive buff to deep olive buff in our material); base not seen, infrequently dichotomous throughout, branches irregularly flexuous, somewhat contorted, about 0.8 mm. in diameter below, slightly compressed and up to 2 mm. wide where the complanate axils of ramuli are nearly opposite, the more slender portions terete, slightly longitudinally rugose from areolation of the cortex which cracks away in places leaving farinose decorticate areas; ramuli somewhat irregularly disposed with complanate axils on the larger axes, less so on the slender ones, often curved, tips acuminate, sometimes blackened, variable in length, fragile.

Apothecia sessile on short lateral branches or near the base of a large ramulus, 3–4 mm. in diameter, nearly plane; exciple slightly impressed; marginal cilia about 12, very variable in length; disc slightly concave, carneous, densely white-pruinose.

Cortex 40–45 μ thick, highly gelified, the outer 15 μ brownish; algal layer 20–25 μ thick, of discrete colonies of *Trebouxia*, cells 6–8 μ in diameter; medulla 40–55 μ thick, of densely woven slender hyphae, heavily nubilated; axis 670 × 490 μ, outer surface eroded longitudinally, appearing solid, but slightly lacerate

with a few narrow bundles of slightly brownish, coarser hyphae, resembling the rays of vascular plants.

Most of our material is rather young and is densely tangled, somewhat smaller in dimensions than the type, but agrees well in essential characters.

SIERRA LEONE: Sugar Loaf, 480 m., *H. Donovan Tindall 16*, at Kew.
GOLD COAST: C. P., Ashanti, Agogo, 510 m., *T. F. Chipp 445*, at Kew.
CÔTE D'IVOIRE: Gommèlé, Agnibile-Krou, *Guy Roberty 13553*, in Herb. Mo. Bot. Gard.
CAMEROONS: Victoria, in Meyer Crater, 2580 m., on *Aquaria salicifolia*, *T. P. M. 917 p. p. min.*, fragment tangled with *Usnea speciosa* Mot., at Kew.

96. USNEA AMANIENSIS Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.

Type: Tanganyika, East Usambara, Amani-Maramba, 1030 m., growing in festoons on the topmost branches of tall evergreen rain-forest trees, *P. J. Greenway 4151*, ex Herb. E. African Agr. Res. Sta., Amani.

Thallus prostrate and creeping along the larger branches of trees, the more slender branches pendent, rigid, more than 60 cm. long, chamois to deep colonial buff; base black, conic, 5 mm. in diameter, buried in humus (decaying mosses, leaves, etc.) and attached to the bark, tapering upward to 1.4 mm. in diameter and about 10 mm. long, then several times dichotomous with short internodes, then rarely dichotomous throughout; principal axes about 1 mm. in diameter, thinning at each dichotomy to the capillaceous summits; short lateral branches or ramuli penetrate the humus and form secondary holdfasts on the underlying bark, giving rise to secondary axes; terete, smooth, without verrucae or tubercles; main axes closely annularly cracked, the cortex regenerating over the crack, producing a white annular appearance of the larger axes, longitudinal cracks rare and the areoles do not crack off; the more slender branches with very narrow annular cracks, sometimes close, sometimes distant on the same branch, terete or with single minute paler verrucae; ramuli 10–20 mm. long, very slender, straight or curved, rather fragile, tips acute, sparsely and minutely tuberculate, no soredia, isidia nor propagula seen.

Apothecia abundant on some axes, absent on others, 3–5 mm. in diameter, cupulate, becoming subplane, sessile on ramuli, eciliate; exciple smooth; disc fuscous, white-pruinose.

Cortex about 55 μ thick, apparently fastigiate but so highly gelified it is impossible to see the structure clearly; algal layer 45 μ thick, of discrete colonies of *Trebouxia* about 30 μ in diameter, forming a nearly continuous layer; medulla 105–120 μ thick, of very densely woven hyphae, so heavily nubilated with minute brown crystals that structure is not very clear; axis 450 μ in diameter, of strands of longitudinal, conglutinate hyphae, lumen 1–1.5 μ in diameter, separated by thin-walled hyphae 6–8 μ in diameter very heavily nubilated with brown crystals (giving a brown reticulate appearance to the transverse section).

The Nyasaland fragment has a single apothecium 9 mm. in diameter, a slightly thicker cortex; the axis appears solid, i. e. the thinner walled cells have not yet

turned brown and are not nubilated. The color of *U. amaniensis* is suggestive of the GLABRATAE, OSSEOLEUCAE, but all the other characters clearly relate it to the ELONGATAE, CERATINAE or LONGISSIMAE.

TANGANYIKA: East Usambara, Amani-Maramba, 1030 m., growing in festoons on the topmost branches of tall evergreen rain-forest trees, *P. J. Greenway 4151*, ex Herb. E. African Agr. Res. Sta. Amani.

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., *L. J. Brass 16845, 16828, fragment* (Vernay Nyasaland Exp., 1946), in N. Y. Bot. Gard. Herb.

97. USNEA EBURNEA Motyka, Frag. Flor. Geobot. 1:29. 1954.

Type: Madagascar, Manakambahiny Est, large wood between Alaatra and Tamatave, near Saharakara River, 800 m., com. *H. des Abbayes*.

Thallus pendent, quite rigid, about 80 cm. long, yellow-stramineous (cream buff in our plant); holdfast a black disc 5 mm. in diameter, surface with radial ridges (coalesced rooting fibers), base 2–3 mm. long, closely annulate, dichotomous at very obtuse angles, soon dichotomous at a 90° angle and occasionally so above with long internodes, axes quite flexuous, very slightly angled, almost terete, rarely with cristate ridges on larger branches, closely annular, terete on more slender branches and less closely annulate; surface with scattered subpapilliform tubercles, sometimes in irregular rows on the larger branches, apparently elongating and breaking off as a rather stout isidium, paler than the thallus; ramuli close except near the base, mostly 10 (–20) mm. long, curved, tapering to an acuminate point, minutely and sparsely tuberculate.

Apothecia not abundant (absent in our material), subterminal on larger ramuli, 2–4 mm. in diameter, concave becoming plane or even revolute, deformed; exciple smooth, eciliate; disc deep flesh color, white-pruinose.

MAURITIUS: without locality or collector, at Kew.

98. USNEA SAVANARUM Duvigneaud, Bull. Soc. Roy. Bot. Belg. 85:112. 1952.

Type: Congo: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud, 582 U4*, in Herb. Duvigneaud, two fragments in Bot. Mus. Lund, loaned by Dr. Ove Almborn.

Thallus pendent, 50 cm. or more long, flaccid, grayish green; holdfast and base not seen; primary axes somewhat flexuous, 0.5 mm. in diameter, subterete, occasionally subangular from slightly elevated isidial scars in rows; surface subareolate-corticate (not scaling in the material studied, perhaps so in the lower portion of the thallus) appearing decorticate from coalescent scars of fallen isidia and minute spinules up to 0.3 mm. long, partly tartareous from protruding medullary hyphae; ramuli 3–5 mm. long, perpendicular, abruptly tapering to acute tips, close, smooth or nearly so, about twice annularly cracked; slender short lateral branches up to 25 mm. long, unequally dichotomous, minutely spinulose, appearing minutely

farinose-tuberculate after the spinules are shed.

Apothecia (absent in specimen studied) 3–4 mm. in diameter; exciple subsmooth to very slightly pitted; marginal cilia few, resembling the ramuli; disc white.

Cortex about 40 μ thick, fastigiate, hyphae 6–7 μ in diameter, lumen 1 μ, gelified, the outer 10 μ heavily nubilated with dark brown granules; algal layer of discrete colonies of *Trebouxia*, about 15 μ in diameter, forming a nearly continuous layer, with some colonies much deeper in the medulla; medulla 30–35 μ thick, of rather densely woven, predominantly radial hyphae, 6–7 μ in diameter, laxer next the axis, heavily nubilated with dark brown crystals, soluble in KOH but not in lacto-phenol; axis solid, brownish, 250 μ in diameter, of conglutinate, longitudinal hyphae, about 4 μ in diameter, lumen about 1 μ; axis K reddish brown; medulla K yellow becoming orange as the solution dries. Transverse sections are promptly bleached by K except for the algal cells.

Occasionally a member of a dichotomy of a short lateral branch is very densely branched, forming a compact cluster 3–4 mm. in diameter, probably teratological. Only two fragments about 10 and 12 cm. long, were available for study. These are clearly from the upper half of a main branch and are clearly corticate throughout, but it is probable that the basal portion of the thallus would show some scaling, due to the thin, laxly woven region of the medulla next the axis.

CONGO: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud 582 U4*, cotype fragments in Bot. Mus. Lund.

99. USNEA INDIGENA Motyka, Frag. Flor., Geobot. 1:27. 1954.

Type: Madagascar, Manakambahiny Est, large wood between Alaatra and Tamatave, Sahamalaza, 800 m., com. *H. des Abbayes.*

Thallus pendent, flaccid, about 30 cm. long, chamois to cream buff; dichotomously branched, the branches curving downward until they are soon nearly parallel as main axes, 0.7–0.8 mm. in diameter, subsequent dichotomies rare, axils complanate, 90°; very indistinctly few-angled, lower portion of axes annulate, smaller branches continuous, terete, smooth, tapering to capillaceous summits; ramuli moderately close throughout, slender, tapering to acuminate tips, mostly 4–10 mm. long, a few longer and dichotomous at their tips, bearing a few minute spinules which break away and serve as isidia.

The ramuli are capable of forming a holdfast where they come into contact with a twig, as a black disc about 1 mm. in diameter.

NYASALAND: Mt. Mlanje, on Likabula Valley track, 1610 m., in *Podocarpus-Widdringtonia* forest on steep rocky slopes, *P. J. Greenway 6332*, ex hb. E. African Agr. Res. Sta., Amani 374/46, at Kew.

MADAGASCAR: Cercle M. des Merie [? illegible], *native collector*, vere 1901, ex herb. H. E. Haase, at Farlow Herb.

100. Usnea contorta Jatta, Malpighia 19:163. 1905.

Type: Madagascar, Piunarantsoa, Beforna, collected by a native.

Thallus pendent, subflaccid, up to 60 cm. long, pale stramineo-green (Motyka), dark olive buff to deep olive buff in our plants; holdfast a thick black disc 5 mm. in diameter, base blackened, 5 mm. long, 1 mm. in diameter, closely annulate, branching closely dichotomous just above the base, axils sometimes complanate, the branches curving and becoming subparallel, very rarely branched above, often one branch larger than the other; axes 1 mm. in diameter, areolate below, sometimes with simple cracks, in other plants the margins of the areoles obtusely elevated, subscrobiculate with predominantly oblique ridges, giving a somewhat contorted appearance, rarely low-tuberculate between as well as on the ridges, more slender branches closely but indistinctly annulate with scattered single tubercles; ramuli irregularly disposed, rare on the lower portions of the main axes, closer above but not crowded, 10–20 (–35) mm. long, faintly tuberculate, some straight, others curved or flexuous, tapering uniformly to acuminate, slightly darkened tips.

Apothecia not abundant, sessile on the more slender portions of a main axis, or more frequently lateral in the middle of a very long ramulus, cupulate, becoming plane; marginal cilia irregularly disposed, quite close, erect, of variable length, similar to ramuli; exciple smooth, margin splitting and becoming crenate; disc pale flesh color, white-pruinose (in some, the thecium has been eaten away by insects and small erect cilia develop on the old disc).

Tanganyika: Southern Highlands, Iringa District, Morgana, 1930 m., *W. Carmichael 296*, in E. African Herb.

South Africa: Uitenhage District in forest, *Ecklon*, ex herb. W. Sonder, in Tuckerman herb. at Farlow Herb.

Mauritius: without locality, *Robillard* ex Gray Herb. at Farlow Herb.

Réunion: Salazie, *Frère Rodriguez*, com. Bouly de Lesdain ex herb. Hasse sub *U. mascarena* Motyka olim herb. nom., at Farlow Herb.

101. Usnea arguta Motyka, Lich. Gen. Usnea Stud. Monog. 406. 1937.

Type: Congo, Congo de Lemba, *Goliat*.

Thallus up to 40 cm. long, rather more rigid than *U. trichodeoides*, pendent, axes pale olive buff when decorticate with isidiose soredia, corticate portions and ramuli olive buff; base not seen; infrequently dichotomous with obtuse axils, the branches curving downward and soon parallel; axes about 1 mm. in diameter below, somewhat flexuous, terete to slightly longitudinally rugose, cortex cracking off and then farinose with abundant isidiose soredia, patches of cortex remaining with minute sorediose verrucae; ramuli quite close, 10–20 (–30) mm. long, the longer subdichotomous, tips acuminate, straight or curved, corticate with minute, irregularly disposed pale tubercles, forming soralia on the longer ramuli, but never as dense as on the axes.

Apothecia (on *Chipp 57* only) sessile on the smaller branches, up to 6 mm. in diameter, nearly plane; marginal cilia few, radiating, 5–10 mm. long, similar to

ramuli; disc flesh color, white-pruinose, becoming nude when old.

Our plants are mostly short fragments about 20 cm. long, but agree with Motyka's description. Perhaps the variable amount of decortication may be correlated with habitat, depending on dryness and wind. Plants referred here from semi-swamp, dense forests are much more corticate than from open scrub woodland and savannas. *Eyles 1023*, a short fragment from the mid-portion of a main axis, is somewhat doubtfully referred here. The axis is mostly corticate and more distinctly rugose than the other plants, but much less so than in *U. aequatoriana* Mot. Curious spinules with dark tips are irregularly borne on some ramuli.

SUDAN: Issore, Onyiro, 3° 50′ N., 32° 50′ E., 1720 m., *T. F. Chipp 57*, more corticate and fertile, at Kew.

KENYA: Chyulu hills, 1290 m., on trees in mixed savanna forest on lava flows, *P. R. O. Bally 1236*, at Kew.

UGANDA: Ruizi River, 1390 m., in riverine forest, *T. Jarrett 402 p. p.*, at Kew.

TANGANYIKA: Bukoba, Kabobwa, Mingiro Forest Reserve, 1550 m., on trees of dense semi-swamp evergreen forest, *G. Watkins 492* (native name: *machankima*), at Kew

N. RHODESIA: E. Isoka District, uplands 1480 m., on trees in *Brachystegia mimosaefolia* scrub woodland, *C. G. Trapnell*, at Kew.

S. RHODESIA: Matapos District, 1610 m., *Frederick Eyles 1023 p. p. min.*, at Kew.

102. USNEA TRICHODEOIDES Vainio, Ann. Acad. Sci. Fenn. A 6^7:8. 1915; emend. Motyka, Lich. Gen. Usnea Stud. Monog. 421. 1937.

Usnea longissima f. *Ebersteinii* Stein, Jahresber. Schles. Ges. Vaterl. Cult. 66:133. 1888.

Type: Cape of Good Hope, com. *Persoon*, in herb. Acharius at Helsinki. Motyka based his description on Tanganyika, Usambara, *C. Holst 2642*. Type of *Usnea longissima* f. *Ebersteinii* Stein, from Tanganyika, Kilimanjaro, Rabai Ndaru in scattered forests in steppes, *H. Meyer*.

Thallus up to 40 cm. long, pendent, very flaccid, ecorticate, axis colonial buff to white, corticate, ramuli deep olive buff; dichotomous just above the holdfast, then rarely dichotomous throughout, the branches soon parallel, straight or slightly flexuous; axis 0.4–0.6 mm. in diameter, slightly thinner at each dichotomy to the capillaceous summits, terete to slightly flattened and occasionally very faintly longitudinally rugose; cortex soon flaking off, leaving a farinose, subsorediose surface on most of the branches except the smallest, sometimes with a few minute spinules (isidia?); ramuli close, somewhat variable in length, 3–10 (–15) mm. long, corticate, terete, smooth, tips acuminate, the longer dichotomous near the tips.

Apothecia (absent from most of our material) subterminal on stouter ramuli, 3–8 mm. in diameter; exciple slightly lacunose to smooth; marginal cilia few, about 10 mm. long, often broken off; disc nearly plane, flesh color, lightly but distinctly pruinose.

The material referred here is rather variable. It differs from *U. arguta* Motyka in having axes more slender (0.4–0.6 mm. instead of 1 mm.), straight rather than tortuous, shorter, smooth ramuli 3–15 mm. long (instead of 10–30 mm.) with

irregularly disposed small sorediose tubercles; axis with pale yellow strands instead of subfuscous axes from strands of fuscous hyphae.

SUDAN: Onyiro, Issore, 1770 m., 3° 50′ N., 32° 50′ E., *T. F. Chipp 57*, a fragment, at Kew.

KENYA: Mt. Elgon, 2790 m., *E. J. Lugard & Mrs. Cyril Lugard 470*, at Kew; Loita plains 40 and 60 miles southeast of Narok, 1610–2250 m., *Anita G. Curtis 669b, 743c*, in Dodge herb. det. Motyka, and at Farlow Herb.; Lake Ngunga, 1775 m., on trees, *G. M. Allen 1788* in Howe herb. sub *U. longissima*, at Farlow Herb.

UGANDA: Ruizi River, 1550 m., *T. Jarrett 402*; Bugishu, Butandiga, 2410 m., *A. S. Thomas 484*; Kigezi, Kasatoro, Kabale River, 2250 m., *I. R. Dale L43*; Mt. Elgon, 1290 m., *W. Small 216*; without locality *H. Fyffe 167*; all at Kew.

CONGO: Mt. Kahusi, ca. 2700 m., on *Arundinaria alpina*, *F. L. Hendrickx 4302*, in E. African Herb.

TANGANYIKA: Bukoba, Kabobwa, Mingito Forest Reserve, 1550 m., *G. Watkins 492* (Forest Dept. Herb. 3231, native name: *machankima*), sheets at Kew and in E. African Herb.; Maruessa between Duruma and Taita, *Hildebrandt* com. C. Rensch ex herb. Sbarbaro, at Farlow Herb.

ZANZIBAR ISLAND: without locality, *J. H. Vaughan 1359*, at Kew.

MOZAMBIQUE: Inhambane, on *Copaifera*, without collector, at Kew.

SOUTH AFRICA: Gnove [?], *Drège*, com. Laurer ex herb. Sbarbaro; Uitenhage District, in forest, *Ecklon*, ex herb. W. Sonder in Tuckerman herb.; both at Farlow Herb.

STUDIES IN THE CAPPARIDACEAE. III

Evolution and Phylogeny of the Western North American Cleomoideae*

HUGH H. ILTIS**

One of the best ways to visualize evolution is to arrange related forms in the order of their complexity. With fairly large and complete series, it is possible to show graphically the homology of unlike extremes by observing the intermediates. Use of the so-called reduction series (Woodson, 1935) such as the modifications described by Bower (1923) and by Zohary (1948) is open to severe criticism, since they are composed of contemporary types not in direct line of descent (Lam, 1951). Nevertheless, they help to elucidate such problems as relationships between species and species groups, direction of evolution, and morphology of derived structures, particularly in cases where paleobotanical and cytogenetical evidence is lacking.

The Capparidaceae, as well as the whole of Rhoeadales, provides a wealth of series illustrating many evolutionary problems (Camp, 1950). Four western North American genera of the subfamily Cleomoideae, namely *Cleome* sect. PERITOMA, *Cleomella*, *Wislizenia*, and *Oxystylis*, constitute one of the most clear-cut "reduction series," and their taxonomy, morphology, geographical distribution, intra- and inter-generic relationships, and intra-specific variations are discussed in this paper. Based on the above, an attempted evolutionary interpretation is correlated with the geologic history of North America and is discussed in the light of the probable great importance of desert evolution in this group and the angiosperms generally.[1]

I. Taxonomy

The Capparidaceae is a member of the Order Rhoeadales, with the Cruciferae its closest, most specialized relative. The 40 genera and 700 species of Capparidaceae, occurring mainly in the tropics of both hemispheres, are customarily separated into two major subfamilies: Capparidoideae and Cleomoideae. The Capparidoideae includes forms, mainly shrubby or arborescent, with fleshy, indehiscent fruits. Its largest genus is *Capparis*, the pickled flower buds of the Old World *C. spinosa* furnishing the capers of commerce, a seasoning for food. The Cleo-

[1] I should like to express my thanks to the Institute of Science and Technology, College of Arts and Sciences, University of Arkansas, and to the Department of Botany, University of Wisconsin, both of which gave me support during the course of this study; also to the Society of Sigma Xi, for a grant-in-aid. Many friends have given me much encouragement and helpful criticism: Drs. G. T. Johnson, R. C. Rollins, L. H. Shinners, and particularly Drs. Royal Shanks and A. J. Sharp, of the University of Tennessee; and Drs. George B. Van Schaack, R. M. Tryon, and R. E. Woodson, of the Missouri Botanical Garden, St. Louis, where a minor portion of the present paper was used as part of a master's thesis (Iltis, 1950). My wife, Grace Iltis, has provided encouragement throughout this study, and her interest and counsel are here gratefully acknowledged.

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moideae are mostly herbaceous and annual, rarely shrubby. The fruits are usually dehiscent, unilocular capsules (siliques) with two generally deciduous valves attached to a persistent replum (placenta). This subfamily includes the small North American genus *Polanisia* and the world-wide genus *Cleome*, with about 180 taxa, 83 of which occur in the Western Hemisphere (Iltis, 1952, 1955b). Of these, some are known for their showy flowers, such as *C. houtteana* Schlecht. ("*C. spinosa*" hort.), the Spider Flower, and *C. serrulata* Pursh, the Rocky Mountain Bee Plant.

SYNOPSIS OF THE TAXA CONSIDERED IN THIS STUDY
(Probable relationships diagrammed in fig. 16)

A. *Cleome*[2] sect. PERITOMA (DC.) Baill.
1. *C. lutea* Hook. (including var. *jonesii* Macbr.)—Yellow Bee Plant, Stinking Mustard
2. *C. isomeris* Greene (*Isomeris arborea* Nutt.)—Burro Fat, Bladder Bush
3. *C. platycarpa* Torr.
4. *C. serrulata* Pursh—Rocky Mountain Bee Plant
5. *C. multicaulis* Sessé & Moc. ex DC. (*C. sonorae* Gray)
6. *C. sparsifolia* Wats.

B. *Cleomella* DC.[3]
1. *C. angustifolia* Torr.
2. *C. longipes* Torr.
3. *C. perennis* Iltis
4. *C. mexicana* Sessé & Moc. ex DC.
5. *C. palmeriana* Jones (a complex including *C. cornutae* Rydb., *C. montrosae* Payson, *C. nana* Eastw.)
6. *C. hillmanii* A. Nels. (including *C. macbrideana* Payson)
7. *C. obtusifolia* Torr. & Frem., *sensu lato*
8. *C. plocasperma* Torr. & Frem. (*sensu* Abrams, 1944)
9. *C. parviflora* Gray (including *C. alata* Eastw., *C. gracilis* Brandg.)
10. *C. brevipes* Wats.

C. *Wislizenia* Engelm.[4]
1. *W. refracta* Engelm. (including all nine species described by Greene (1906) and others.)—Jackass Clover, Stinkweed, Spectacle Pod

D. *Oxystylis* Torr. & Frem.
1. *O. lutea* Torr. & Frem.

II. GENERAL MORPHOLOGY

The eighteen species enumerated above share such a large number of vegetative and floral characters that it is sometimes difficult to distinguish between flowering plants of two genera. All species are small or medium-sized plants (figs. 4–6), annual (except *Cleome isomeris*, *Cleomella perennis*, *C. mexicana*, and, rarely, forms of *Wislizenia*), though not always ephemeral, and are essentially glabrous (except *Cleome platycarpa* and *Cleomella obtusifolia*). The leaves are compound, with 3 (in *Cleome lutea* 5) entire leaflets less than 6 cm. long, succulent and thick, more or less conduplicate and often glaucous, these usually tipped by a thick, usually varnished mucro or by a slender scarious hair.

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[2] A comprehensive monograph of *Cleome* in the New World, written as a doctor's thesis, is awaiting publication (Iltis, 1952).

[3] In the only published revision of *Cleomella* (Payson, 1922), the species concept is too narrow. Crum's (1929) unpublished thesis was useful in my studies, which cover all species except *C. angustifolia* and the *C. palmeriana* complex.

[4] The many variants here are best divided into the eastern *W. r.* var. *refracta*, the northern *W. r.* var. *melilotoides* (Greene) Johnston, and the southwestern *W. r.* var. *palmeri* (Gray) Johnston (cf. Johnston, 1924). Kuntze (1903) considered *Wislizenia* a section of *Oxystylis*.

One significant peculiarity of all but two taxa *(Cleome isomeris, C. platycarpa)* is the possession of microscopic whitish, filiform or laciniate, scarious stipules[5] on either side of the petiole base or, in ebracteate flowers, at the base of the pedicel (figs. 7–8). These stipules are inconspicuous, and commonly break off in old stems. Their frequency emphasizes close relationship, since in other Cleomoideae such structures are found only in a few species of *Cleome* and rarely in *Polanisia.* Morphologically, they seem to be homologous to the minute, gland-like stipules of the Resedaceae, concerning whose nature there have been so many divergent views (Bolle, 1936). In the opinion of Hennig (1929) they are probably reduced stipules. The presence of these anomalous structures is additional evidence of relationship between the two families.

The tetramerous, usually weakly zygomorphic flowers, borne in racemes (figs. 4, 5, 8) are characterized by frequent occurrence of persistent or tardily deciduous, synsepalous calyces, by sessile or subsessile petals, and tightly coiling mature, dry anthers. The flowers, in general, are larger in *Cleome* than in the other genera. The petals are yellow in all species except the purple or pink *Cleome serrulata* and *C. multicaulis,* and have a convolute (closed) aestivation. A structure that varies considerably is the more or less eccentric nectariferous disk between corolla and androecium which is highly complex in some species. All species seem to be insect-pollinated (Pellett, 1930; Jepson, 1936).

The truncate or pointed stigma (in *Cleome multicaulis,* somewhat capitate) and the slender, indurate style (fig. 3) point to the general specialization of this group, since I consider sessile, capitate stigmas as primitive. This view agrees with that of Zohary (1948) regarding the Cruciferae.

The seeds vary in size and ornamentation, but in structure are basically uniform, being reniform, globular to ovoid, somewhat flattened and characterized by a deep invagination, with the embryo, as in all Cleomoideae, curved and notorhizous (conduplicate). The two parallel ends, or "claws," may remain open (as in *Polanisia* and most Old World species of *Cleome*), or they may be fused exteriorly by a thin membrane or the thick testa, as in nearly all New World Cleomoideae. In the four genera treated here the two "claws" are fused internally as well, save at the very tip. The lack of a cavity inside the seed is also a specialized condition, for in primitive tropical species, e.g., *Cleome parviflora* or *C. spinosa,* the internal sinus between the claws is large. All species inhabit semi-arid or arid regions of western North America (figs. 9, 12), such as deserts, semi-deserts, sagebrush *(Artemisia)* associations, alkali flats, and grasslands, occurring often in "badlands" and in gravelly or sandy, dried-up river beds and shores. Most species occur in alkaline and saline soils, with some definitely halophytic.

In summary, the uniformity of most vegetative and floral structures justifies the assumption of this as a coherent group of closely related taxa.

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[5] The "stipular" thorns or spines of *Cleome* and *Capparis* are apparently epidermal outgrowths, not foliar in nature.

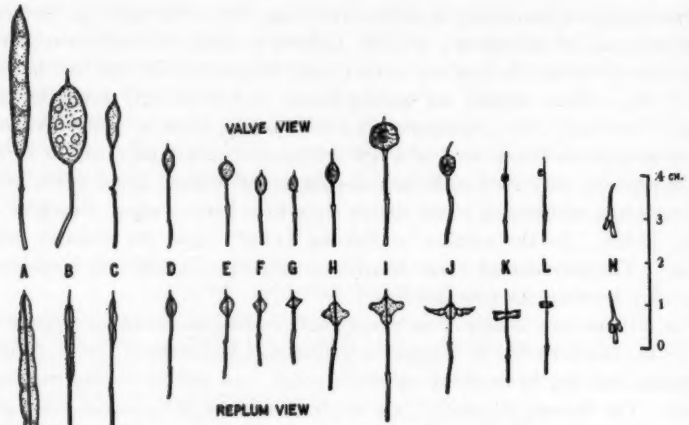

Fig. 1. Fruit reduction series of the North American Cleomoideae:
A, *Cleome lutea*; B, *Cleome platycarpa*; C, *Cleome multicaulis*; D, *Cleome siliculifera* (Brazil); E, F, *Cleomella palmerana*; G, *Cleomella plocasperma*; H, *Cleomella obtusifolia*; I, *Cleomella hillmanii*; J, *Cleomella obtusifolia* var. *taurocranos*; K, *Wislizenia refracta* var. *palmeri*; L, *Wislizenia refracta* var. *refracta*; M, *Oxystylis lutea*.

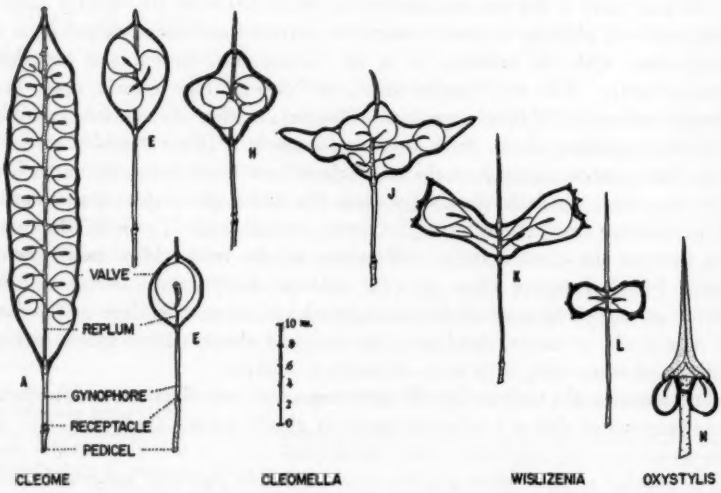

Fig. 2. Silique reduction series of the North American Cleomoideae. Letters correspond to those of fig. 1.

III. Morphological Basis for an Assumed Generic Phylogeny

The fruits, racemes, and stipules of the four genera discussed may be arranged in phylogenetic series, in which we can follow each from *Cleome*, through *Cleomella* and *Wislizenia*, to its greatest modification in *Oxystylis*.[6]

1. *Modification of the Fruit.*—

The changes are most striking in the fruit. Indeed, this "reduction series" suggested the current study.[7] The basic fruit type of the Cleomoideae is the silique, but of the four genera only *Cleome* has siliques, a fruit type that is considered primitive in this family as well as in the whole order (Zohary, 1948).

All species of *Cleome* sect. PERITOMA have dehiscent siliques formed by two valves attached to an elongated replum on which the 8 to 30 or more seeds grow. When the fruits are ripe the valves fall off, permitting the seeds to fall free while the replum remains attached to the plant (fig. 10A). Interjected between silique and receptacle is the gynophore (fig. 2), a slender stalk 5–40 mm. long. Both gynophore and pedicel elongate somewhat after flowering. Some Cruciferae have similar siliques except that a false septum is drawn across the replum making the pod two-chambered.

The siliques of two *Cleome* species may help us to understand the evolution of the *Cleomella* silicle. (1) *Cleome lutea*, primitive as the only species with five leaflets, has fruits that vary from only 8 mm. long in depauperate plants of var. *lutea* to 80 mm. in var. *jonesii*. In the short fruits and general habit, var. *lutea* at times strongly resembles *Cleomella angustifolia* and *C. longipes*. (2) *Cleome platycarpa*, primitive in its floral structure but otherwise specialized, has siliques anomalous in their strong compression (fig. 1B), with flat valves attached to a broadly oval replum tipped by a long style. A roundish replum, rare in *Cleome*, is usual in *Cleomella*. Hence, in replum shape *Cleome platycarpa* is intermediate between *Cleome* and *Cleomella*. Young plants of *Cleome platycarpa* closely resemble those of *Cleome hillmanii*, a similarity probably due to convergent or parallel evolution.

Cleomella fruits (fig. 4) are *silicles*, short siliques not much longer than wide. The repla are oval to round (fig. 1 E–J, top row), similar to those of *Cleome*, but wider and smaller. Viewing the fruits from the side (fig. 1 E–J, bottom row), however, we find a variety of shapes caused by lateral expansion of the valves, ranging from hemispheres to obtuse or acute cones or horns (fig. 1J). Some *Cleomella* species may have fruits very similar to the unrelated South American *Cleome siliculifera* Eichl. (fig. 1D) or abnormally small-fruited *C. lutea*. As in *Cleome*, the seeds fall free (fig. 10B).

The tendency of *Cleomella* valves to expand laterally correlates with: (1) the

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[6] Evidence for establishing the generic phylogeny of *Cleome* and *Cleomella* was derived mainly from the morphology of the primitive taxa in each genus. Nevertheless, the phylogeny within a genus, particularly in *Cleomella*, is worth noting since many trends from primitive to specialized species are homologous to and parallel those of the series *Cleome* → *Oxystylis*.

[7] I am grateful to my esteemed teacher, R. E. Woodson, Jr., who interpreted for me this sequence, thus introducing me to the concept of "reduction series" (Woodson, 1935).

obvious decrease in length of gynophore, pedicel, and fruit (½ to 1/20 the length of *Cleome* siliques), particularly in the Great Basin species; and (2) the radical decrease in seed number (2–12 (–20) per silicle, cf. fig. 2). Here, while decrease in fruit *size* is accompanied by only a minor decrease in seed *size*, the seed *number* decreases markedly. By contrast, in other groups of *Cleome* with reduced siliques (West Indian "UNIFOLIOLATAE"; North African sect. THYLLACOPHORA Franch.), seed size is usually directly proportional to silique size, with the seed number essentially constant.

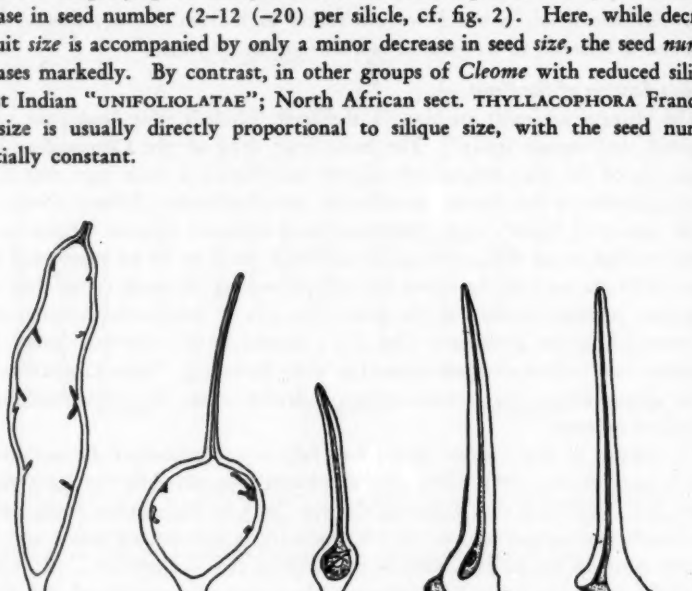

Fig. 3. Longitudinally sectioned fruits (i.e., gynophore-replum-style) after removal of valves and seeds.

Most variable in fruit shape is the Californian *Cleomella obtusifolia*, with obtusely conical valves in the typical form (fig. 1H) to narrowly conical ones in var. *taurocranos* (fig. 1, and 2J). In this most specialized fruit of *Cleomella* the valves are constricted at intervals. Due to this a single seed is often loosely imprisoned in the tip of each valve (fig. 10C), the valve and seed falling together at maturity—a rather insignificant and accidental matter were we to stop at this point! However, what we see is a feeble expression of an evolutionary tendency, hereafter called the "schizocarp tendency" which reaches great prominence in *Wislizenia* and *Oxystylis*.

The polymorphic, monotypic *Wislizenia* (fig. 5) differs sharply from *Cleomella* in fruit characters, the evolutionary trends already apparent in *Cleome* and *Cleomella* (figs. 1 and 2, K–L) being greatly increased. Thus, the repla, reduced to minute rings 1 mm. in diameter, tipped by long, slender styles (fig. 3), are borne on gynophores and pedicels, each only 5–12 mm. long. Because of the small replum, the shape of *Wislizenia* valves differs from those of *Cleomella*. Valves of *Cleomella* are hemispheric to narrowly conical, being *widest at the point of attachment to the large replum* and narrowest at the apex, while those of *Wislizenia* vary from obovoid or subspherical to obconical, being *narrowest near the point of attachment to the tiny replum* and widest near the middle in obovoid valves (fig. 1L) or at the apex in obconical ones (fig. 1K).

Thus, when the fruits mature, each valve permanently encloses its one or two seeds (fig. 10D). In *Wislizenia*, then, the fruit is really a schizocarp, with each of the two valve-seed units a mericarp. These could be thought of as nutlets, in which all but the seed tip (which may project partially through the basal pore of the valve) is enclosed by the ovary wall. We have here a continuation of the schizocarp tendency indicated in *Cleomella obtusifolia* var. *taurocranos*. Of the four ovules in each ovary, *usually only two mature into seeds*, although all may develop in the larger-fruited, primitive *W. r.* var. *palmeri*. This low seed number is a continuation of the trend already manifest in *Cleomella*.

The valves of var. *palmeri* are obconical and elaborately ornamented, while those of var. *melilotoides* are obovoidal and nearly smooth. However, the latter not only reach ultimate size and valve reduction, with but one seed in each valve, but the valves also resemble those of *Oxystylis*, the final genus in this sequence, in having small rounded mericarps with tightly held seeds. Furthermore, while both *Cleomella* and *Wislizenia* usually have divaricate valves, some races of the specialized northern *(melilotoides)* and eastern *(refracta)* varieties have valves which point unilaterally away from the plant, resembling those of *Oxystylis* (fig. 1L, top row).

Oxystylis lutea (fig. 6), endemic to the Death Valley region, shows to what high degree a generalized structure such as the Rhoeadalean silique may become modified. While its seeds and valves resemble those of *Wislizenia r. melilotoides*, the structure of style, replum, gynophore, and pedicel is radically different. The replum of *Wislizenia* (fig. 3) is a tiny ring. In *Oxystylis* (figs. 2 and 3), this ring undergoes great lateral and downward expansion and thickening, resulting in an "inverted V-shaped" tube with down-facing open ends (fig. 2M). From this modified "replum" a greatly thickened, elongated, spinescent style projects upward. The gynophore and pedicel, each about 1 mm. long, are also much stouter and shorter than in *Wislizenia* (fig. 8C, 8D).

Attached to the down-facing orifices of the replum are the two parallel and unilaterally protruding, obovoidal valves (figs. 1M, 6, 8D). Like those of *Wislizenia r. melilotoides*, they enclose their single seed tightly and permanently (fig. 10E), with but a minute pore at their attachment point. However, the thinner

and very smooth *Oxystylis* valves fit the seeds like seed-coats, which, functionally, they are.

We have traced the fruit modifications from *Cleome* through *Oxystylis*: (1) from large, elongate siliques, through round or laterally pointed silicles with divergent horizontal valves, to small schizocarps with nearly vertical, unilateral valves; (2) from fruits with many free-falling seeds to fruits where each valve and its single seed are inseparably joined and fall as one unit; (3) from fruits with short, slender styles and large elongated, hoop-shaped repla to those with long, spinescent, stout styles and small, tubular, "inverted V-shaped" repla; and finally (4) from elongate pedicels and gynophores to fruits in which these structures are short, stout, and nearly obsolete.

2. *Modification of Racemes and Bracts.*—

We may trace the modifications of racemes and bracts from primitiveness in *Cleome* to specialization in *Oxystylis*. The primitive Cleomoid inflorescence is a bracteate raceme. Through loss of bracts, ebracteate types have evolved independ-

Fig. 4. Open bracteate inflorescence of *Cleomella angustifolia*. Note long region of vegetative growth before flower production.

Fig. 5. Dense ebracteate inflorescences of *Wislizenia*.

ently at different times, with both bracteate and ebracteate racemes occurring in several genera (various groups of *Cleome* and in *Podandrogyne*). The ebracteate type generally characterizes specialized taxa.

Racemes are bracteate in *Cleome* sect. PERITOMA. One species *(C. multicaulis)* has 3-foliolate leaves not specially differentiated into bracts and of the same size and shape whether subtending flowers or not. In the other species of PERITOMA, however, all but the lowest bracts are 1-foliolate and easily distinguished from the multifoliolate cauline leaves.

Because racemes tend to be densely flowered at the apices and young bracts are very small, inflorescences may at first appear to be ebracteate. However, in time the bracts become foliaceous and after flowering the raceme axis elongates greatly, spacing bracts as well as the pedicels, so that the lower, older portions of a raceme are open and clearly bracteate (fig. 8A). Of the many flowers in each raceme, most are deciduous, only a few ovaries remaining to mature into siliques at well-spaced, cyclic intervals. Most older bracts therefore subtend only pedicellar scars.

Since *Cleome* racemes are indeterminate inflorescences, they continue apical growth for months, becoming quite long, over 6 dm. in some species. The individual racemes are clearly separate.

Racemes and bracts in *Cleomella*, particularly in the primitive *C. longipes* and *C. angustifolia* (figs. 4 and 8B) are much like those in *Cleome*. In some specialized species 3-foliolate bracts, which look like cauline leaves, occur throughout (*C. brevipes, C. obtusifolia, C. mexicana;* cf. Iltis, 1956). In other species a *tendency toward bract reduction* is quite evident, and racemes are often apically ebracteate.

Plants of *Cleomella* tend to be smaller and more branched than those of *Cleome*. Their racemes, though separate, are more clustered and usually appear after less vegetative growth. Fruiting racemes are denser, for many more flowers mature into silicles.

In *Wislizenia* (figs. 5 and 8C), racemes are *always ebracteate*, sometimes resembling nearly bractless extremes of certain *Cleomella* species *(C. longipes)*. Some forms of *W. r. refracta* or *W. r. melilotoides* have profusely branched stems, each branch tipped by a raceme 1–2 cm. long (fig. 5). From this specialized type we can go all the way to the primitive var. *palmeri* where little-branched stems bear a few racemes 10–20 cm. long.

Mature racemes of *Wislizenia* are very crowded (fig. 8C), because up to 95 per cent of the flowers develop into fruits, while at the same time the raceme axes elongate only slightly after flowering. Though these inflorescenses are structurally racemes and therefore indeterminate, they are determinate in that they grow often less than 1 or 2 cm. in *W. r. refracta* and *W. r. melilotoides*, before growth is curtailed.

If a lateral branch system of *Wislizenia* (lower right, fig. 5), with its many short inflorescences, were telescoped into a head-like "bur" about $\frac{1}{10}$ its original size, one of those peculiarly congested, axillary, compound inflorescences characteristic of *Oxystylis lutea* (fig. 6) would be obtained. Each of these raceme clusters

is borne singly in the axil of a well-developed leaf, and each leaf, *even the very first*, subtends such a cluster. The center of each cluster is composed of one to several stout, short, straight or branched central axes from which diverge 5–15 stubby side branches, densely covered with flowers or fruits. Each side branch, rarely over 1 cm. long, represents a raceme and may bear as many as 40 flowers though not all develop into fruit (fig. 8D,E). That this congested multitude of racemes is homologous to a branch system of *Wislizenia* is further borne out by the occasional occurrence of a large, normal leaf on the central axis at the base of one of the side branches (fig. 6, bottom right hand "bur"). Such leaves correspond to those usually found in *Wislizenia* at the base of each raceme.

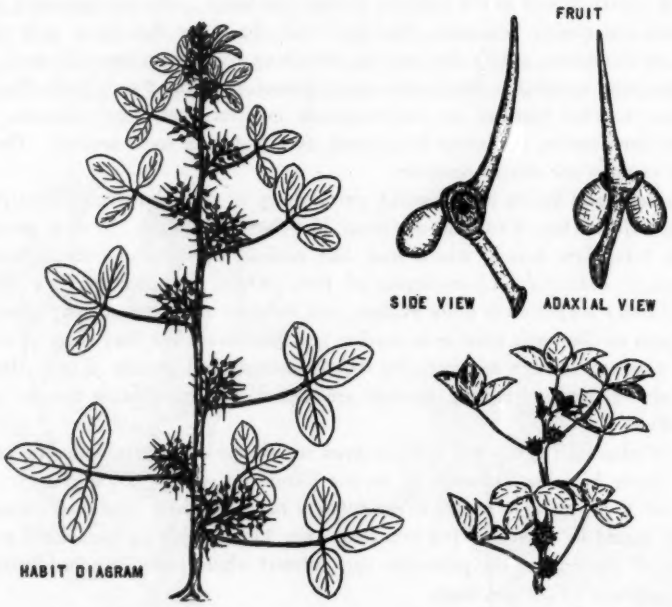

Fig. 6. Highly congested ebracteate inflorescence clusters of *Oxystylis*. Plant on right, with mature fruits; plant on left, very young and in flower (after Jaeger, 1941). Note exceedingly short region of vegetative growth before flower production.

The high development of four tendencies is responsible for the uniqueness of the *Oxystylis* inflorescence: (1) the essentially determinate, short growth of racemes; (2) the nearly total lack of post-floral elongation of raceme axes; (3) the almost complete elimination of non-floral sections of branch systems; and (4) the early initiation of flowering.

Thus again we have traced modification from primitiveness in *Cleome* to specialization in *Oxystylis*.

3. *Modifications of the Stipules.*—

We can trace modifications of stipules from *Cleome*, in which they are generally lacking, through *Cleomella* and *Wislizenia*, with progressively larger stipular bristles, to their eventual fusion into the flat complex structure in *Oxystylis*. Their occurrence in sixteen of the eighteen species under discussion emphasizes the phyletic coherence of the genera.

All species of *Cleome* sect. PERITOMA, except *C. isomeris* and *C. platycarpa*, have scarious, yellowish, bristle-like stipules, from 1–2 mm. long, occurring either

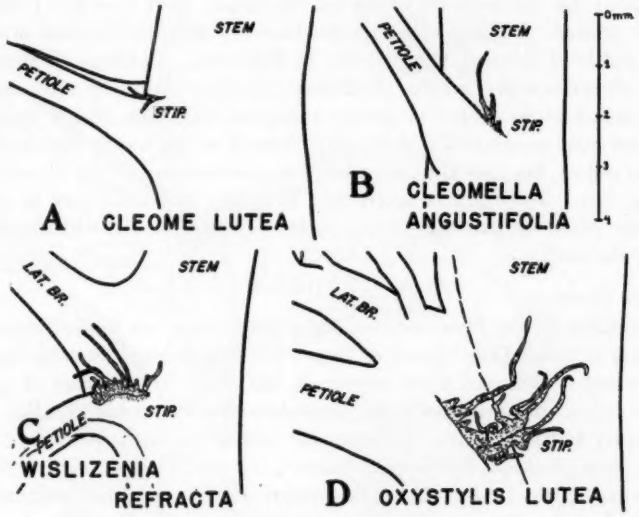

Fig. 7. Stipules of cauline leaves.

singly or in tufts of 2 or 3, on either side of the petiole base, of both cauline leaves and bracts.

Stipules of *Cleomella* generally resemble those of *Cleome*, but in some species tend to be longer (1–4 mm.), each tuft having 3–8 bristles. The largest are those of *C. obtusifolia*, noted by Watson (Gray, 1895), who erroneously cited the absence of stipules in all other species as a key character! Jepson (1936) made a similar error.

As in *Cleomella*, stipules in *Wislizenia*[8] occur in tufts each having up to 10 basally joined bristles of unequal length.

[8] These are the only stipules of the Cleomoideae regularly mentioned in the literature (Munz, 1935; Jepson, 1936; Pax and Hoffman, 1936).

In *Cleome* and *Cleomella* stipules are associated with the petiole bases of both the cauline leaves and flower-subtending bracts. *Wislizenia* and *Oxystylis* have cauline leaves with stipules but *no bracts!* Yet on the axis of the inflorescence, just beneath each pedicel base, well-developed stipules are found in the place where the petiole of the bract-blade would have originated were the inflorescence bracteate. This loss of blade and petiole but retention of stipules is an interesting case of unequal reduction of an organ. Furthermore, although the stipules on the inflorescence occur occasionally as two separate tufts, usually they are fused into a single prominent strip which makes them more conspicuous than in the two bracteate genera.

Oxystylis has the most specialized and the largest (2–4 mm. long) stipules of the four genera.[9] The other three genera have bristles which increase in number, length, and basal cohesion, from *Cleome* to *Wislizenia*. In *Oxystylis* these trends reach a climax in rather peculiar structures (fig. 7D): flat, very thin, and transparent central blades with 3–8 greatly contorted, flagellate, slender teeth. The stipules are most abundant and most easily observed on the stubby bractless racemes (fig. 8, D and E), but they also occur paired on the stems at the base of each cauline leaf (fig. 7D). They may be interpreted as groups of bristles such as occur on *Wislizenia*, joined for half their length to form the flat lamina, with the free ends forming the teeth.

4. *Other Trends.*—

In addition to the fruit, raceme, and stipule, there are less-prominent series which may be traced from *Cleome* to *Oxystylis*. Among these are reduction in size of flower and of seed, and minor changes in leaf shape. A summary of primitive versus advanced characteristics in the Cleomoideae has been published (Iltis, 1956).

Contrary to Bessey's dicta, the perennial habit of *Cleomella perennis*, *C. mexicana*, of some plants of *Wislizenia r. palmeri*, and of *Cleome isomeris* is definitely *not* primitive (Iltis, 1956). It can be interpreted as a specialized secondary character which in the Cleomoideae appears sporadically in several groups of grassland and desert species through convergent evolution.

IV. Interpretations of the Reductions and their Relations to Aridity

A study of the plant's environment considered in conjunction with its morphology may help to interpret the structural trends of the North American Cleomoideae from the primitive (*Cleome* sect. PERITOMA) to the most specialized genus (*Oxystylis*).

1. *Distributions in Relation to the Prevailing Climate.*—

The distribution of the four genera corresponds roughly to prevailing climatic patterns in western North America (figs. 9, 12). The comparatively unspecialized sect. PERITOMA of *Cleome* is widespread, occurring generally in more mesic regions,

[9] Despite the large size and peculiar structure of *Oxystylis* stipules, botanists have failed to notice them; some have even stated that they are lacking (Jepson, 1936).

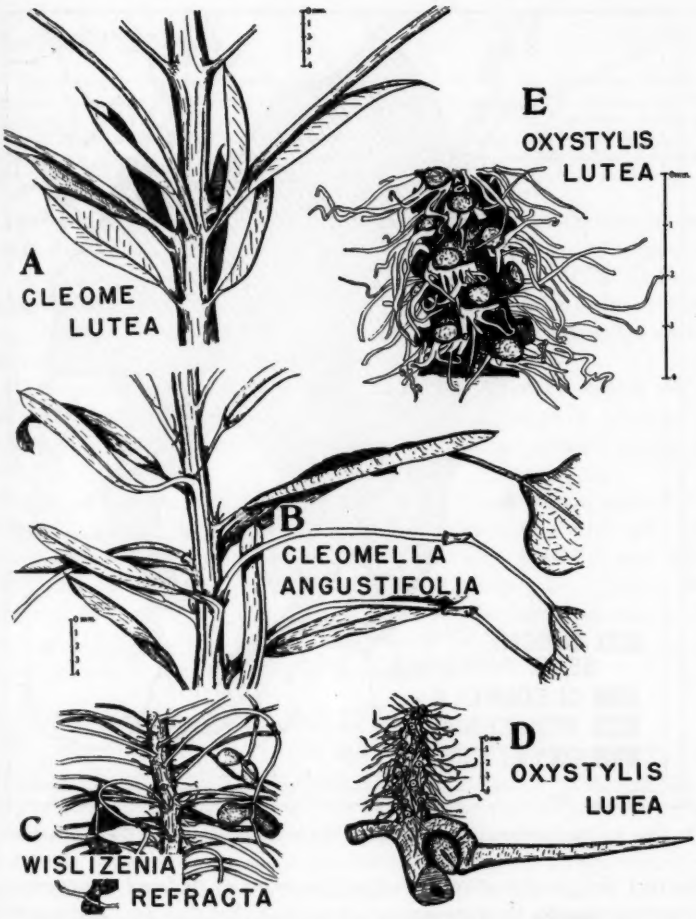

Fig. 8. Portions of inflorescences with stipules: A–D, drawn on same scale; E, enlarged portion of D. Note progressive condensation of raceme axis and increase in stipule size and length.

in less alkaline habitats, and at higher elevations. The more specialized genera, *Cleomella and Wislizenia,* occur in progressively more arid and alkaline habitats of lower elevations, and the most specialized genus, *Oxystylis,* is limited to the most arid and alkaline area of the continent, the Death Valley region of California and Nevada. This correlation between arid climate and morphological specialization[10]

[10] This applies not only to the generic level! The most specialized species within *Cleome* sect. PERITOMA *(sparsifolia)* and in *Cleomella (obtusifolia, parviflora, brevipes)* are likewise associated with some of the most alkaline, arid habitats of California and Nevada.

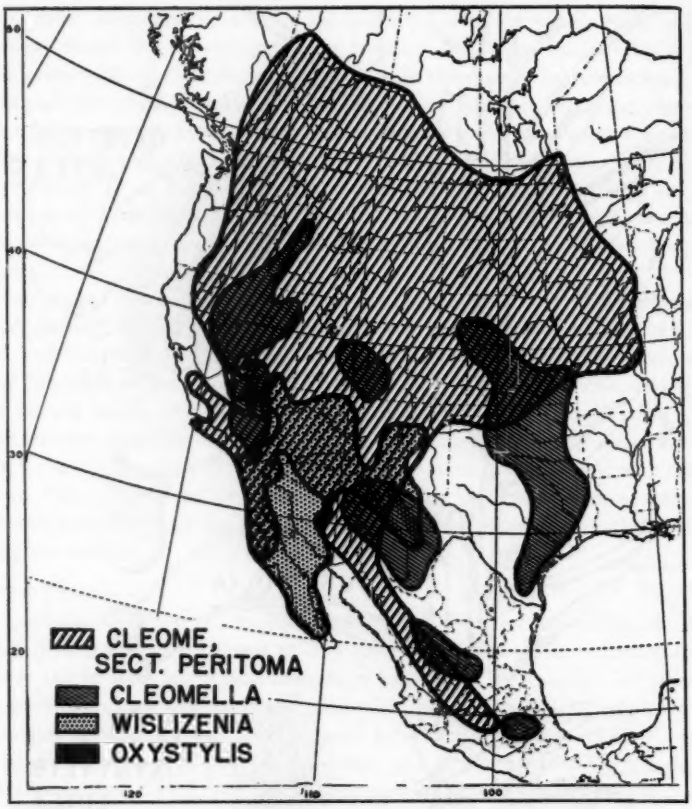

Fig. 9. Total distribution of the western North American genera of Cleomoideae.

implies *that these modifications are related in some way to desert environment*, and it is tempting to make the conventional assumption that they are "adaptations" and have "survival value".

2. *Climatic Notes, Especially on Death Valley and the Mojave Desert.*—

In nearly all environmental aspects, Death Valley is extreme (Thompson, 1929; Anon., 1954; Went, 1955). According to Munz (1935):

> The [mean?] temperature in the Mojave Desert is about 100° F., this prevailing between five and eight months out of the year. The extreme temperature of 134° F. at Greenland Ranch in Death Valley has been reported. Except in higher areas, the rainfall does not exceed five inches and often is under three inches. In Death Valley, which is 296 [282 according to Anon., 1954] feet below sea level, the lowest point in the United States, *two inches of rain is a maximum* [4.2 in 1941, the wettest year (Went, 1955)], *and a minimum of zero is of frequent occurrence*. The entire desert climate is one of unusually high summer temperature with resulting low humidity and high evaporation. [*italics* mine]

Coville (1893) states:

> The observations on the temperatures of Death Valley in 1891 for the hottest month of the year, July, show an average daily maximum of 116°, an average daily minimum of 87°, and a mean of 102° F. A maximum temperature of 122° occurred five times during the summer; these temperatures were taken under cover of a shelter constructed especially to eliminate the effect of radiation from the ground . . . In direct sunlight bodies that readily absorb heat must reach a temperature many degrees in excess of the recorded maximum.

According to Parish (1930) the record of 134° F., "when the mercury rose to the top of the tube", would have been exceeded in an instrument of greater range, and "such temperatures in the shade would indicate at least 150° F. in the sun". This temperature "is the highest natural-air temperature that has been recorded on the earth's surface by means of a tested, standard thermometer exposed in a standard ventilated instrument shelter" (Thompson, 1929).[11]

Soil temperatures must be even higher. MacDougal (1908) reports 148° F. in sandy soil surrounding roots of annuals at the Grand Canyon in Arizona. On a sunny summer day, soil temperatures in Death Valley must certainly greatly exceed 148° F.!

Precipitation varies from year to year, with the average annual rainfall (Went, 1955) 1.35 inches. Over a ten-year period (Thompson, 1929) the average monthly rainfall during November (0.20″), January (0.48″), and February (0.40″), accounted for 64 per cent of the yearly precipitation. During the rest of the year only rarely was there rain in excess of 0.10 inches per month, and in 64 out of 114 consecutive months there was no rain whatever. The rains that do come are usually in the form of hard, short showers.

3. *Some Prerequisites for Desert Survival.*—

With the environment so extreme and water supply so limited, a plant has to be specially adapted to survive; in short, it has "to make hay while it rains". The ability of seeds to take up water quickly after one of the rare showers, rapid germination, a short life cycle,[12] economy in growth and transpiration, and as rapid and large an output of seeds as the circumstances permit are all adaptations which seem essential to survival of desert annuals. The fruit and raceme modifications of the xerophytic Cleomoideae seem to have "developed in response to" two of the major demands of a desert environment: (1) the immediate and rapid germination of the seed during the rare times when water is available, and (2) the subsequent most rapid, most direct (or most economical) completion of the life cycle, i.e. production of seeds.

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[11] This world record was recently exceeded in Tripoli (136.4°, fide Anon., 1954).

[12] Dr. W. F. Blair (personal communication) tells me that in some Anura (e.g. *Scaphiopus*, the spadefoot toads) the length of the immature aquatic phase of the life cycle is generally correlated with aridity of native habitat. Toads in mesophytic areas reach the adult stage after many months of larval existence, while those in some parts of Texas complete metamorphosis in as short a time as twenty days.

4. *Xerophytic* vs. *Mesophytic Cleomoideae.*—

The differences between mesophytic and xerophytic Cleomoideae, of both Old and New World (cf. Iltis, 1956), may be generalized as follows: *Mesophytes*, as a rule, are 1–6 m. tall, have fewer, thinner, larger leaves with 3–13 narrowly elliptic, flat leaflets with long-attenuate apices, and produce flowers after considerable vegetative growth. Their fruits, commonly borne on long gynophores, are usually 5–10 cm. long (some 25 cm.!) and usually produce many fairly large seeds. The number of mature fruits per plant is frequently low. *Xerophytes* are rarely over 2 m., usually less than 1 m. tall, and have many small leaves. The 1–3 (–5, or rarely more) leaflets are often conduplicate, with obtuse to rounded or emarginate apices, those of the American species generally glaucous and fleshy. Some species flower and fruit when only 10 cm. tall; the Saharan *Cleome scaposa* may fruit when only 3 cm. tall (Kachkarov and Korovine, 1942) and *Cleomella brevipes* when only 1 cm. tall (Iltis, 1955b). The small fruits, often 0.5–3.0 cm. long, have many small seeds or few larger ones. The gynophore, often lacking or short, frequently reflexes over the pedicel. The number of mature fruits per plant tends to be very high. The above generalizations apply to most desert Cleomoideae, including such widely separated, unrelated groups as the western North American species, the West Indian "unifoliolate" species of *Cleome*, the Eurasian *Cleome* sect. THYLLACOPHORA Franch., etc. The occurrence of these characteristics in widely separated groups of desert plants is evidently due to convergent, adaptive evolution (cf. Briquet, 1914).

5. *Interpretations of the Reductions.*—

Most species of *Cleome* sect. PERITOMA and the primitive taxa of *Cleomella* (fig. 4) grow tall, have many leaves, greatly accrescent, bracteate inflorescences (fig. 8A) and large, many-seeded fruits, all structures requiring relatively large quantities of water and organic materials, and long growing seasons.

Most taxa of *Cleomella* (fig. 4) are smaller and often more branched than those of *Cleome* sect. PERITOMA. Inflorescences are shorter and frequently nearly ebracteate, and may appear earlier in the life cycle. The fruits are smaller, have fewer seeds, and mature more rapidly. The earlier appearance of flowers and the smaller fruit would result in shorter, or more economical life cycles.

Young plants of *Oxystylis* flower almost immediately after germination, with the earliest inflorescences in the axil of the first or second foliage leaf, an inch or less above ground (fig. 6). Compared with primitive species of *Cleome* or *Cleomella* (fig. 4), these plants do not waste time or water on much vegetative growth. The stems of *Oxystylis* are usually "unbranched"; its leaves are few. The inflorescences do not grow indefinitely as in Cleome, but after flowering they elongate at most a few millimeters, in sharp contrast to the striking postfloral elongation of the peduncle in most other Cleomoideae (fig. 8). Since the two-seeded fruits are very small, maturation is rapid. The lowest inflorescences of a plant 3 dm. tall may carry nearly mature fruits while the upper are still in flower.

To summarize: The series from *Cleome* sect. PERITOMA to *Oxystylis* shows

progressively less vegetative growth, increasingly early flower production, and more rapid maturation of fruits, the latter reflected in the reduction of fruit, pedicel and gynophore length, and in inflorescence elongation (cf. fig. 8). That these are adaptive modifications seems obvious. For example, if a 3 dm. tall *Cleome serrulata* should perish through environmental vicissitudes, it would probably leave no seeds to perpetuate the species, while even smaller plants of *Oxystylis* would have mature seeds. To quote Parish (1903):

> It is in these other areas that there is the greatest development of the protective adaptations which enable a plant most fully to utilize a scanty supply of water. The methods by which this is effected are three: by habits of growth; by provisions for storing supplies of water and food in times of plenty as reserves for times of need; and by contrivances for diminishing the loss of water through evaporation.
>
> The first of these methods is well exemplified by most of the xerophytic annuals. They spring up at once after light rains and put forth no more than a leaf or two before proceeding to the production of a flower and a fruit. If moisture now fails, reproduction is assured; should it continue to be supplied, branches are sent out and flowers and seed multiplied. Thus a plant when receiving only a little moisture may fulfill the cycle of existence and provide for the continuance of its species, without attaining an inch of stature; but under more favorable conditions it may attain dimensions of two or three feet.

Any change, therefore, that resulted in more economical vegetative growth and consequently more rapid production of flowers and seeds in some of the ancestral populations of *Cleome* sect. PERITOMA would have been advantageous either to their survival in a climate becoming progressively more arid or in the invasion of more arid regions. Those populations of *Cleome* that adapted to aridity by reducing the length of vegetative and fruit-producing periods appear to have given rise to *Cleomella*, whose ancestors, by the same process, produced *Wislizenia* and *Oxystylis*.

That reduced silique size probably evolved as a result of selection favoring shorter maturation periods and not for other reasons of economy, such as seed number reduction *per se*, is borne out in another way. In some species of *Cleomella*, and particularly in *Wislizenia* and *Oxystylis*, reduction in number of seeds from each flower is compensated for largely *by the much greater number of flowers that mature into fruits*. In fact, in some plants of *Wislizenia* nearly every flower produces fruits (fig. 8) which clothe the inflorescence so densely that the total number of seeds is greater than that of most plants of *Cleome*.

6. *Interpretation of the Schizocarp Tendency.*—

The evolution of the fruit reductions appears to have been indirectly associated with that of the schizocarp tendency in *Wislizenia* and *Oxystylis* where one or two seeds are permanently enclosed by the ovary wall (valve) (figs. 2, 10). This additional "seed coat" might help the plant to survive in deserts since it facilitates water uptake and retention, resulting in rapid seed germination, a well-known characteristic of desert plants. Thus, Bell (1953) reports a minimum germination time of nineteen days for a desert species and twenty-nine days for a mesophytic species of *Sanicula*. Seed germination in desert areas is necessarily closely tied up with rare, short and often violent showers.[13] At other times, according to Coville (1893),

[13] A discussion of seed germination in Death Valley and its relation to hard rains is given by Went (1955).

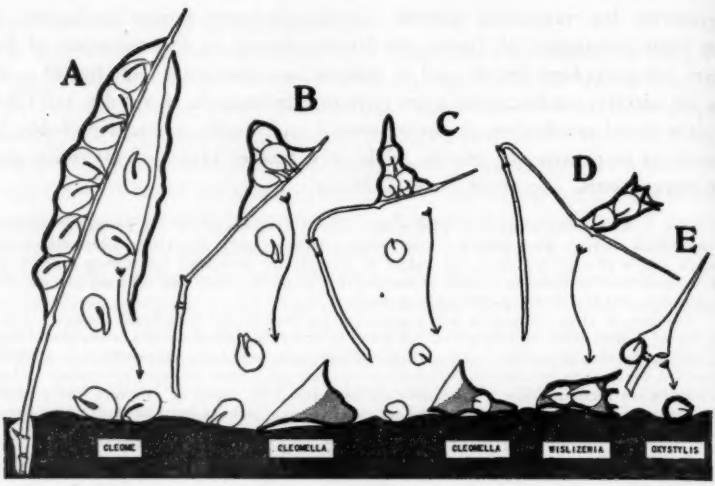

Fig. 10. Dehiscence of fruits and evolution of schizocarp tendency: A, *Cleome lutea* var. *lutea*; B, *Cleomella longipes*; C, *Cleomella obtusifolia* var. *taurocranos*; D, *Wislizenia refracta* var. *palmeri*; E, *Oxystylis lutea*.

water is practically non-existent since rain water quickly re-evaporates into a very dry atmosphere or is soaked up by a parched earth.

The ovary wall *appears* to function in two ways: (1) the soft tissues of the valve imbibe water and swell (fig. 10 C–E, black areas); (2) by capillarity, water enters through the mouth of the urceolate valve and fills the narrow spaces between valve and seed (fig. 10 C–E, black dots). Imbibition is probably of secondary importance in the development of the schizocarps since many Cleomoideae with free-falling seeds already have an outer testa with large blister-like cells which swell up when wet, thus retaining water for a time (e.g. *Cleome serrulata, C. lutea, Cleomella hillmanii* in North America; *Cleome arabica*, with very long, elongate hair cells, in the Sahara, etc.) Capillarity, however, appears to me to have been important in the schizocarp evolution. *We may postulate* that the tendency started in an ancestral *Cleomella* with fruits like those of *C. obtusifolia* var. *taurocranos* (fig. 10C), where one seed is loosely held by a constriction near the tip of the funnel-shaped valve. If such a valve falls off and becomes filled with water, the captive seed will have more water available for a longer period and hence a greater advantage over the free-falling seed in the availability of sufficient water to commence germination. Such a hypothetical race gave rise to *Wislizenia*. Here the valve is urceolate with a small basal opening, through which, on immersion, water enters, filling all spaces between the seeds and valve wall, the latter, in addition, becoming soft and spongy (fig. 10D). The one or two seeds are thus held in a water-filled "pitcher" which dries out slowly.

If this interpretation is correct, selective forces that furthered seed inclusion must have acted during the earliest germination phases of the life cycle. In contrast, selective forces that produced smaller fruit and foreshortened branches must have acted on later stages: vegetative growth, flowering, and fruit maturation. The two sets of adaptations, though produced by independent selection factors during different stages of the life cycle, are nevertheless historically interconnected since such schizocarpous fruits *could not have been produced* from *Cleome* siliques *unless preceded by drastic size reduction.* Not until fruits were as small and as laterally expanded as those of *Cleomella* was there any chance for the valves to curve around and imprison seeds. The fruit-size reduction from *Cleome* to *Cleomella* was then a prerequisite, a *preadaptation,* on which the schizocarp tendency of *Wislizenia* and *Oxystylis* was based.

7. *Differential Selection and the Critical Phase of the Life Cycle.*—

That fruit-maturation and pre-germination are the phases of the life cycle in these xerophytes during which selection pressures are greatest is suggested by the pronounced modification of fruits and racemes, and by the relative lack of modification in most other plant parts. In the Cleomoideae, desert survival is evidently not as closely tied up with the floral phases. The flowers, though specialized, are similar in all the genera, without any pronounced morphological trends as in the fruits or racemes, save decrease in size. There are sporadic instances of highly specialized floral structures, such as petal-nectaries *(Cleome sparsifolia)* and various specialized nectariferous disks *(Cleome* and *Cleomella).* The thickish leaves, generally adapted to xerophytism and similar throughout, were changed only slightly, mainly from narrow and pointed to broad and emarginate leaflets.

These specific points agree with the generalizations of Stebbins (1949) that in sedentary plants "problems connected with reproduction and dispersal are far more important than those involved with maintenance". They also agree with many examples given by Stebbins of families (Gramineae, Cruciferae, etc.) in which flowers and leaves vary little, while fruits and inflorescences show a wealth of modifications.

Although the interpretations of the reductions are mostly conjectural, it would not be difficult in the Southwest to obtain data on the exact length of life cycle phases of each taxon, or to compare length of germination of artificially freed seeds of *Wislizenia* with that of seeds enclosed by valves.

8. *Orthoselection.*—

It is evident from the morphological series (fig. 1) that we are dealing with a kind of orthogenesis, *in the descriptive sense only,* which can be interpreted as the result of *orthoselection* (Huxley, 1943). This assumes that the same environmental forces that produced *Cleomella* continued on (though in increasing intensities) to produce *Wislizenia* and *Oxystylis,* and that if the same selective forces are operating on the same phyletic material, the same adaptive trends will continue.

Furthermore, a decreased gene pool resulting from high selection would seem to permit a group to evolve only within the limits of its available genetic potential.

9. *Classification of Modifications.*—

Timofeeff-Ressovsky (1940) classified morphological evolutionary trends into three groups:

(1) *Neutral,* which cannot be interpreted as *obvious* adaptations, there being no plausible relation between structure and environment. The larger stipules, or the tendency of the gynophore to deflex over the pedicel (*Wislizenia, Cleomella* spp.) are placed here though they might be consequential to certain other adaptive trends.

(2) *Adaptive,* where a plausible relationship between morphology and environment is evident. Most reductions studied here appear to belong to this group.

(3) *Harmonious modification.* In examining fruiting racemes of *Wislizenia* or *Oxystylis,* it is obvious that raceme foreshortening could not have taken place with large siliques but became possible after the fruits were reduced in size. Conversely, the many fruits could not have matured if the siliques were large because of spatial interference and problems of nutritive supply. Likewise, bract reduction is also prerequisite to foreshortening for there is not enough space for each *Oxystylis* flower to be supplied with a bract. Another "harmonious reduction" is the decrease in flower size with greater raceme density.

V. Geographic Distribution

1. *Geographical Distribution of the Genera and the Degree of Allopatry or Sympatry of the Species.*—

Cleome, with 180 taxa, is of almost world-wide tropical and sub-tropical distribution (fig. 11).[14] Of the 55 species and 25 subspecies indigenous in the Western Hemisphere, most are tropical. The six species of sect. PERITOMA are restricted to temperate, rarely subtropical, North America (figs. 12A, 13A) with their center of variation in eastern California and adjoining Nevada, where four species occur. All six species are to some extent sympatric, some with an overlap of ranges that is complete or nearly so.

The total range of *Cleomella,* (figs. 12B, 13B) though smaller than that of *Cleome* sect. PERITOMA, is similar in outline. The distribution of individual species is rather different. The five eastern and Mexican species are allopatric with sharply separated ranges. On the other hand, the Great Basin and Pacific slope area, with five species, contains many regions where two or three species occur together, but only one small region in south-central California, the center of variation of *Cleomella,* where four species are sympatric.

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[14] Distribution maps have been plotted from material of major U. S. herbaria (Iltis, 1955b), particularly the Missouri Botanical Garden Herbarium, and from sources that list individual localities, such as floristic works. Especially helpful was the unpublished thesis of Ethel Crum (1929), dealing with *Cleome isomeris, Cleomella* and *Wislizenia,* which cites many specimens. A microfilm copy of this work was kindly supplied to me by the University of California library through Miss Annetta Carter, to whom I should like to express my thanks. Generalized ranges, as given in floras, were found to be unreliable and were not used.

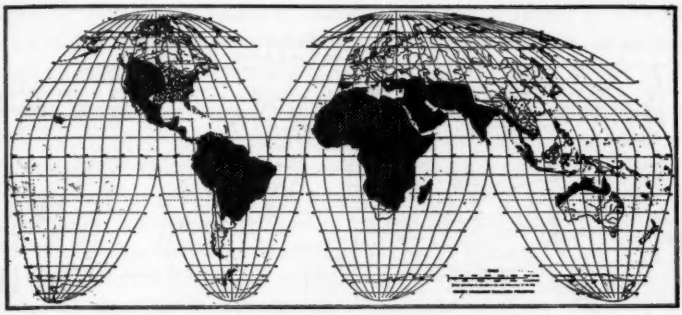

Fig. 11. Distribution of the genus *Cleome*: black with white dots, indigenous; black dots, adventive. Old World, about 90 taxa; New World, 79 taxa.

Wislizenia refracta occurs in the Southwest and adjoining Mexico. Its range is smaller than that of *Cleomella* and appears to be more or less continuous (figs. 12C, 13C), forming a horseshoe around the northern end of the Sierra Madre Occidental. *Wislizenia* spread as a weed into the San Joaquin Valley and other parts of California during historic times (Jepson, 1936), so that its natural range is smaller than the present-day, artificial range. Its morphologically diverse populations appear to be allopatric.

Oxystylis lutea is limited to deserts and washes of the Death Valley region in California and Nevada (fig. 12D, 13D). Most collections come from the Valley itself along the Amargosa "River" (marked on fig. 12D by a black line) where the species is reported to be abundant (Jaeger, 1941). A few specimens have been collected further north in Nevada. *Oxystylis* is a monomorphic taxon, and its populations are, therefore, allopatric.

The total generic ranges progressively decrease in size from the generalized *Cleome* sect. PERITOMA to the specialized *Oxystylis*. The regions in which the most widely distributed group (PERITOMA) occurs are generally rather mesic, while those of *Cleomella*, *Wislizenia* and *Oxystylis* are progressively more xeric, with *Oxystylis* thriving in the driest and hottest climate of the continent.

As to the geographic distribution within a genus, taxa in *Cleome* sect. PERITOMA are very highly sympatric; in *Cleomella* both sympatric and allopatric; and in the monotypic *Wislizenia* and *Oxystylis* the taxa (being the more or less differentiated populations) are allopatric.

2. *Geographic Distribution and Origin of Genera.*—

Taxa frequently evolve through geographic separation of one part of a population from another, and subsequent genetic and morphological differentiation of either or both of these isolated populations through different or unequal selection pressures (Mayr, 1942). That part of the original population which is isolated in

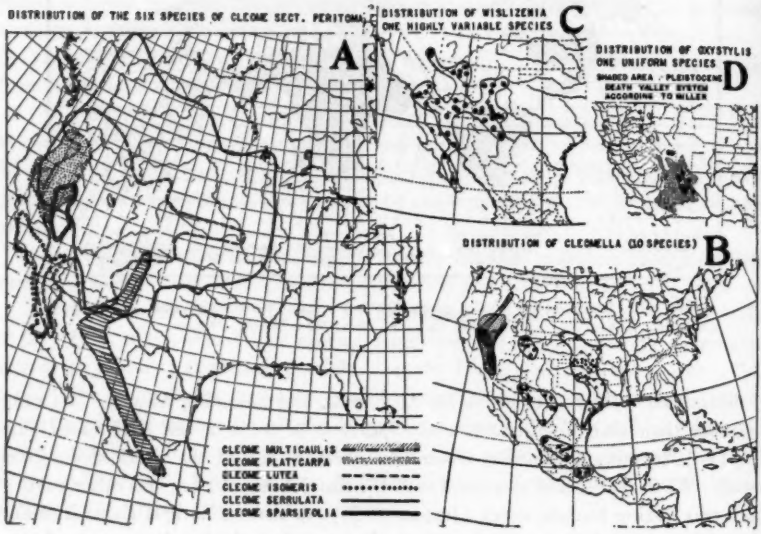

Fig. 12. Distribution of all taxa in the western North American Cleomoideae and the degree of sympatry and allopatry in each genus.

an environment fast changing to a more xeric one will evolve rapidly. The other part, if its environment does not markedly change, may remain more generalized and will evolve slowly. Generally, the more primitive taxa (subspecies, species, genera) will be found in the more mesic climates, the more specialized in more xeric ones. If two taxa have thus evolved from one original population through geographic isolation they would *at least for a time* occupy allopatric ranges. By deciding which of the two related taxa is more specialized and which more primitive we can speculate on the geographic direction of evolution and on the geographic origin of taxa. That such a scheme is applicable only to relatively recent evolution need not be emphasized (cf. Deevey, 1949).

Wagner's ideas as amplified in "Jordan's Law" or "Rule of Proximity", that "given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort" (Cain, 1944), has been found to apply chiefly to species or subspecies within the same genus. The fact that it apparently also applies to related genera, or to closely related species, one in one genus and one in another, greatly extends Jordan's Law. However, such complementary ranges appear here too frequently to be accidental. In the western North American Cleomoideae, the geographic ranges of the two most closely

related taxa of two related genera or, sometimes, the total ranges of two related genera, are highly allopatric, a trend that appears congruent with the phylogeny as outlined on morphological grounds.

Cleome.—The geographic origin of the genus *Cleome* is unknown, though the apparently primitive species occur in the New World tropics. Sect. PERITOMA is similar to some New World *Cleome* species and apparently has been derived from them. The occurrence of *C. multicaulis* in central Mexico (fig. 12A) suggests that section PERITOMA as a whole originated in the Mexican highlands, one of the two important distribution centers of *Cleome* in the New World (the other being South American), the area from which Madro-tertiary elements of the southwestern flora appear to have originated (Munz, 1935; Chaney, 1947; Axelrod, 1948). The total range of PERITOMA is allopatric to that of the other sections[15] of *Cleome* (fig. 13A).

In spite of the fact that the range of PERITOMA overlaps that of *Cleomella* nearly completely (fig. 9), offering little help in tracing the origin of *Cleomella*, we can profitably compare the ranges of the most *Cleomella*-like species of *Cleome* sect. PERITOMA *(Cleoma lutea)* with those of the most *Cleome*-like species of *Cleomella* (the midwestern *Cleomella angustifolia* and the Mexican *C. longipes*). All are very much alike in habit, inflorescence, and seed structure. *Cleome lutea* is clearly allopatric to both species of *Cleomella*, although its range nearly touches theirs in two places (fig. 13B).

The range of *Wislizenia* complements that of *Cleomella* (fig. 13C) except for a major overlap in northern Mexico and adjacent New Mexico and Texas. The two most closely related taxa of the two genera are *Cleomella longipes* and *Wislizenia r. palmeri* (a southwestern, primitive variety). Both are allopatric, being separated by the northern Sierra Madre Occidental. We can postulate, as shown by arrows in fig. 13C, that *Wislizenia* originated in western Sonora, from a branch of *Cleomella* (similar to *C. longipes* ?) isolated by the rising Sierras, and subsequently migrated north and east. Eventually, as *W. r. refracta*, the genus spread through the wide gap of the continental mountain axis in southern Arizona and New Mexico, thus reentering the territory of its ancestors *(C. longipes)*, where the two genera are now sympatric.

Wislizenia and *Oxystylis* are exactly allopatric (fig. 13D), their dividing line the "Death Valley drainage-Colorado River drainage" watersheds (Miller, 1950; Hubbs and Miller, 1948). *Wislizenia*, to my knowledge, has never been collected or reported from the Death Valley region (Coville, 1893, and others).

The above data suggest the origin of these genera as follows (fig. 13A–D): *Cleome* sect. PERITOMA evolved from a mesophytic Mexican *Cleome*. In some drier regions, perhaps in northern Mexico, southern Arizona, New Mexico or western Texas, one of the taxa of *Cleome* (*C. lutea* ?) gave rise to *Cleomella* which

[15] Except for the unifoliolate species and *Cleome tenuis* Wats., which belong to a section (to be named in the near future) more closely related to Old World taxa than to any of the New World.

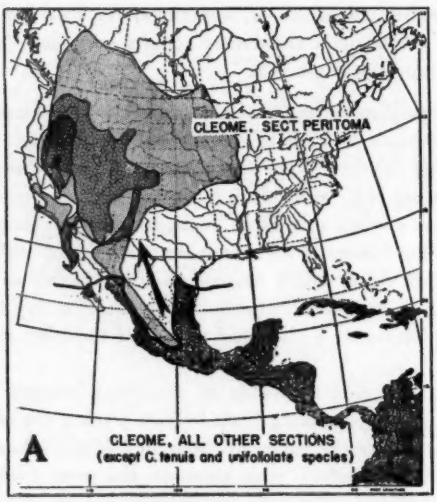

Fig. 13. Geographic distribution and origin of genera. Arrows point from the less specialized to the two most closely related taxa, one in one genus and one in the other.

spread and evolved into many species. The more primitive species apparently remained in the mesic regions with little climatic change, while the more specialized evolved mainly in the California and Nevada deserts and in the Mexican plateau (Iltis, 1956). A southwestern primitive population of *Cleomella* (C. *longipes* ?) spread to Sonora and California and evolved into *Wislizenia* which, spreading north and east, evolved a number of variants. One of these (*W. r. melilotoides* ?) became isolated in the Death Valley region, where it evolved into *Oxystylis*.

Although the center of variation (region with the most genera or species) for the western North American Cleomoideae lies within southern California and Nevada, their putative centers of origin appear to be more to the southeast. This supports Cain's (1944) contention that the two types of generic centers are not necessarily synonymous.

VI. Degrees of Inter-Generic and Inter-Specific Relationship and Intra-Specific Variability

Any systematist knows that there are different kinds of genera, just as there are different kinds of species. These differences between genera are in part due to variations in: (1) the degrees of inter-generic relationships within a group of closely related genera; (2) the degrees of inter-specific relationships; and (3) the intra-specific variability.

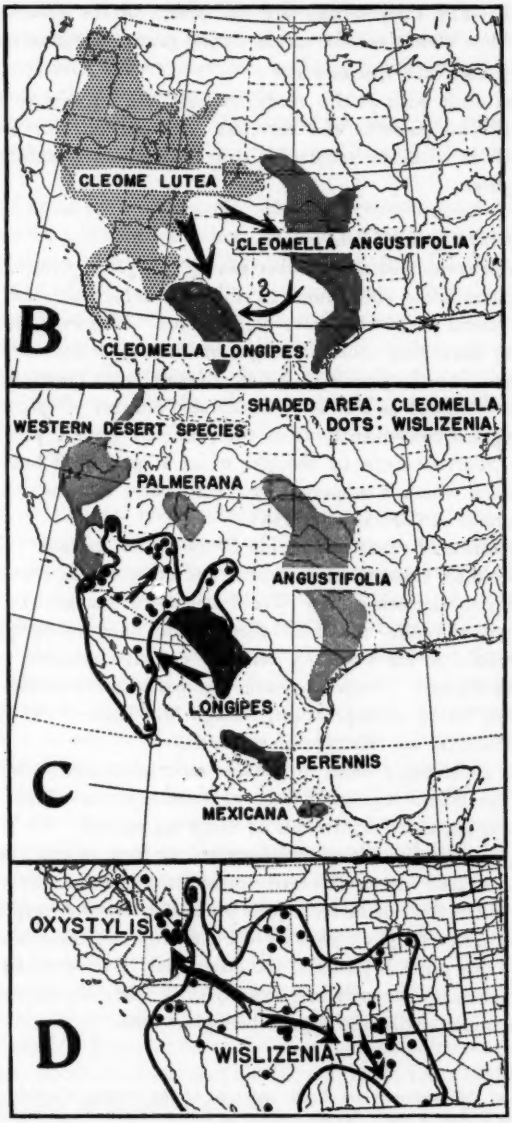

Fig. 13 (Continued). Heavy line in D encloses the Death Valley drainage system.

We can ask: (1) How closely are the genera in the group related to one another?; (2) How closely are the species in one genus related to each other?; and (3) How much does each species vary?

For the taxa dealt with in this study, at least, the answers to these questions fall into well-defined patterns and correlate with the phyletic series previously discussed as well as with the geographic distribution and therefore prove significant to phylogeny.

(1) *Degrees of Inter-generic Relationships.*—

Cleome can be considered the "mother genus," the *genus primordioides* or *primitivus* of the Cleomoideae (Buxbaum, 1951), from which all other genera in the subfamily, the *genera progressiva*, have been derived. Whatever primitive relatives *Cleome* still may have, they must be sought in the Capparidoideae[16] or, preferably in other families. As the primitive genus, *Cleome* contains the least specialized taxa within the subfamily as well as a considerable number of specialized ones that cannot be segregated conveniently from the primitive generic plexus. Thus, the natural section PERITOMA can be thought of as a specialized branch within the genus, a contention which is supported by the allopatry of PERITOMA with respect to the other sections of *Cleome* (fig. 13A).

The exact position of PERITOMA within *Cleome* is not certain. The fused claws of the seed, the closed, convolute aestivation, and other characters indicate a fairly close relationship to the other New World species of the genus. Although the species of PERITOMA do not differ from these by any outstanding qualitative characters, they do differ in the way they combine various characters which occur in diverse groups of *Cleome*. Hence, a generic segregation of PERITOMA from *Cleome*, although natural, would be impractical, though McVaugh (1945) has made just such a recommendation for this type of situation.

Cleomella is exceedingly close to *Cleome* sect. PERITOMA. Biologically, it is nothing but a specialized segment of the PERITOMA plexus which, because of its short, transversely expanded fruits, can be easily segregated. While there are two rather tenuous, quantitative differences between the two genera, the only qualitative difference, and then not an absolutely constant one, is the transverse expansion of the valves. If the fruit of certain, quite unrelated, South American species were placed in this sequence (e.g., *C. siliculifera* Eichl., fig. 1D) there would be no way of telling where one genus begins and the other ends. However, in North America, the break between *Cleomella* and PERITOMA is fairly sharp, and *Cleomella*, a useful genus, is undoubtedly also a good biological unit.

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[16] The members of this subfamily are shrubs and trees of the tropics; in nearly all characteristics of fruit and seed, as well as in many flowers and leaves, they appear to be, if anything, more *specialized* than the Cleomoideae, from which, contrary to current opinion, they may have been derived.

Wislizenia has close affinity with *Cleomella*, although it is not as close as between *Cleomella* and *Cleome*, with *at least* three quantitative differences (reduction of seeds, bracts, replum) and one complex, qualitative difference (shape and ornamentation of the fruit) to separate the genera.

Oxystylis differs sharply from *Wislizenia* by *at least* three quantitative characters and two qualitative ones (extreme modification of replum; telescoped inflorescences).

Assigning one point for each "simple" quantitative inter-generic difference and two points for each qualitative difference, the morphological discontinuity between any two genera follows a trend from *Cleome* to *Oxystylis*, with three points or less between *Cleome* and *Cleomella*, about five points between *Cleomella* and *Wislizenia* and seven or more points between *Wislizenia* and *Oxystylis*. Although this arbitrary point system takes into account only the more obvious characteristics, the relative values are essentially correct as shown by fig. 1. This progressive increase of inter-generic difference, approximately represented by the numbers 3–5–7, suggests some accelerative type of evolution which will be discussed toward the end of this paper (cf. fig. 15B).

(2) and (3). *Degrees of Inter-specific Relationships and Intra-specific Variability.*—*Cleome* sect. PERITOMA is composed of six species so very distinct that some botanists have deemed it necessary to establish segregate genera for them: *Isomeris* Nutt. (for *C. isomeris*); *Carsonia* Greene (for *C. sparsifolia*); *Peritoma* Nutt. (for *C. lutea*, *C. serrulata*, and *C. multicaulis*); and *Celome* Greene (for *C. platycarpa*).

Variability within the species of *Cleome* is not uniform. Some, such as *C. platycarpa*, *C. multicaulis* and *C. sparsifolia*, all taxa with comparatively small ranges, are monomorphic. Others, such as the widespread *C. serrulata* and *C. lutea*, vary considerably, mainly in silique shape and length. *Cleome lutea* is the only species easily divisible into geographic varieties, with *C. l. lutea* widespread and *C. l. jonesii* Macbr. occurring from central Arizona to Baja California. That this divisible species is also the most primitive taxon of PERITOMA is significant. *Cleome isomeris*, highly variable in fruit shape, has been divided into three geographic varieties which overlap and intergrade and are difficult to maintain.

The ten species of *Cleomella* are more closely related to ane another and compose a more tightly-knit group than do the six species of *Cleome* sect. PERITOMA. Flowering plants of different species of *Cleomella* sometimes are almost indistinguishable, a situation not encountered in PERITOMA. Great variability in fruit shape or in pedicel and gynophore length is characteristic of some species, as in the relatively widespread *C. plocasperma* or the more local *C. palmerana* and *C. obtusifolia*. Most other species are monomorphic (Crum, 1929; Iltis, 1955b, 1956). No species is divisible into geographic varieties.

Differences of opinion regarding subgeneric (i.e. subspecific) divisions within *Wislizenia refracta sensu lato* are due largely to the great variability in shape, size,

ornamentation and divergence of fruiting valves and in the length of the raceme. While the specialized smaller-fruited, obovoidal- and smooth-valved plants generally occur in the eastern *(W. r. refracta)* and northern *(W. r. melilotoides)* parts, and the primitive larger-fruited, obconical- and spiny-valved plants (var. *palmeri*) in Baja California and Sonora, the variability does not lend itself easily to taxonomic resolution. The many local races apparently replace each other complementarily (Greene, 1906), without much of a break in morphological pattern. Ten species of *Wislizenia* have been described to date (Greene, 1906). Jepson (1936) considers all, except *W. palmeri*, as varieties of *W. refracta*. I. M. Johnston (1924) interprets the genus as monotypic and very variable, recognizing three geographic varieties, while Crum (1929) considers the primitive and specialized extremes and the intermediates as separate species, all subdivisible into a number of weak varieties. *Wislizenia refracta sensu lato* is indeed highly polymorphic. It deserves to be studied by the methods of modern systematists.

Specimens of *Oxystylis lutea* are not common in herbaria and information about its variability rests on meager evidence. I have examined sixteen different collections, usually several plants in each; it is doubtful whether very many more have ever been made. If there were any appreciable variability among them it was not apparent.

VII. Discussion

Any phylogenetic interpretations of the facts of morphology, geography and variability are highly subjective. In the words of Lam (1951) they "*may* have evolutionary significance, but . . . represent *no* phylogeny, for the simple reason that these schemes are always one-time schemes, with no fossils whatever involved". A different viewpoint, stressing the value of phylogenetic series to the understanding of taxonomy, is that expressed by Buxbaum (1951), with whom I concur.

1. *Correlation of Geographic Distribution and Intra-generic Relationships with Morphology to Determine the Relative Age of a Genus.*—

The fruit, raceme and stipule morphology indicates that *Cleome* is the primitive member of this sequence and that *Oxystylis* is the most advanced; in other words *as genera Cleome* is the oldest and *Oxystylis* is the most recent. The direction of evolution is thus inferred and the relative age of each genus is implied on morphological grounds. Is it possible to correlate patterns of geographic distribution and degrees of intra-generic relationships with the morphological evidence?

The distinctiveness of species in *Cleome* sect. PERITOMA indicates that we are dealing with very old taxa. The species, as we know them, may be young, but the point of divergence of the evolutionary lines that have given rise to these species dates far back in time. Not only are these species very distinct morphologically, but the high degree of sympatry in the group indicates they must also be very distinct genetically (fig. 12A, 13A), for in many places two or three species grow side by side without the slightest indication of hybridization or introgression. For

instance, in the alkaline semi-deserts of the San Luis Valley of southern Colorado, *Cleome serrulata* and *C. multicaulis*, the only species in the section with purple flowers and, in some ways, closely related, grow together with branches intermixed and flowers often touching. Yet, despite careful searching, there was no evidence of hybridization. At Vernal, Utah, *Cleome serrulata* and the very similar *C. lutea* grow in abundance on the same slope. Mass collections by Edgar Anderson show no evidence of introgression!

It is almost axiomatic to declare that sympatric species, as a rule, are old. They have to be, for only after prolonged isolation are two sibling species likely to be sufficiently differentiated that they can exist side by side without re-merging. Therefore, geographically evolving populations have to be allopatric before they can become sympatric (Mayr, 1942).

One would expect then that the genus *Cleomella*, with a *Cleome*-like group as its morphological prototype, would be younger than *Cleome* in other ways as well, and that this age difference would be reflected in the geographic distribution of the species. A glance at fig. 12B shows that this is true. Of the ten species of *Cleomella*, five are allopatric and five are more or less sympatric. As one would also expect in a younger genus, the species of *Cleomella* are usually much more closely related to each other than are those of *Cleome*. Also, the ranges of some of the allopatric species (e.g., the Mexican taxa) still bear the earmarks of having evolved from a once-widespread species through disjunction and subsequent differentiation (Iltis, 1956).

The hypothetical wide-ranging species differentiating into smaller units has passed out of existence in *Cleomella*. However, it is well-exemplified by the "super-species" *Wislizenia* which in its distribution is in a younger stage of evolution (fig. 14). The genus has a single widespread species with a scattered but not markedly disjunct range (fig. 12C). It is highly polymorphic, each of its many populations differing from the next only in minutiae. One series of populations, the southwestern var *palmeri*, is morphologically distinct enough to be called a variety, a subspecies, or, by some, even a species. Most of the other local races are so similar to each other that they have not always been dignified with even subspecific recognition. In studying the diverse fruits, one can almost "see" this species in an active stage of evolution, differentiating into smaller, more local units. Since these populations appear to replace each other geographically, the intraspecific (i.e. intra-generic) allopatry is complete.

Oxystylis, the most specialized and advanced genus morphologically, is youngest in its distribution-variation patterns. With one possible exception, its range is nearly continuous, and the variability within its single species negligible.

The following table gives the number of species in each genus with overlapping ranges (per cent of sympatry).

The sequence is quite clear: from the primitive genus with large, overlapping ranges and very distinct species, through the next genus with smaller, partly over-

lapping, partly separated ranges and more or less closely related species, through the third genus with small allopatric ranges of closely related populations, to the last, most specialized genus *Oxystylis*, where the single species is so uniform morphologically that ranges for individual populations cannot be plotted.

If we start the sequence *backwards* from the youngest to the oldest, we can, in a sense, "see" the evolution of a genus exemplified by the accompanying conceptual scheme (fig. 14). Thus, a genus would have to start in an "*Oxystylis*" stage to get to a "*Cleome*" stage.

Genus	Number of species	Per cent of sympatry	Kinds of taxa
Cleome 6 spp.	1 sympatric with 1 species 1 " " 2 " 2 " " 3 " 1 " " 4 " 1 " " 5 "	17 33 50 67 83	Species exceedingly distinct; ranges often large or medium
Cleomella 10 spp.	5 sympatric with no species 1 " " 2 " 2 " " 3 " 2 " " 4 "	0 20 30 40	Species distinct to very closely related; ranges medium to small
Wislizenia 1 sp., 3 or more subsp. divisions	1 sympatric with no species	0	Taxa (populations and geographical varieties) closely related; ranges small and local
Oxystylis 1 sp.	1 sympatric with no species	0	Taxa (populations) uniform; ranges of individual populations cannot be delimited on morphological grounds because of uniformity

2. *Willis's "Age and Area".*—

When the ranges of all four genera are plotted on the same map (fig. 9), they are seen to *roughly* follow a pattern of what has been called "progressive equiformal areas". Centering essentially around the range of *Oxystylis*, the ranges of *Wislizenia*, *Cleomella*, and *Cleome* sect. PERITOMA become progressively larger. Such a pattern seems, on the surface, to fit perfectly into Willis's (1922) ideas of "Age and Area". According to this theory, the youngest genus, *Oxystylis*, would occupy the smallest range because it has had little time in which to spread its seeds; the oldest genus, *Cleome*, would occupy the largest range because it has had eons of time in which to spread from its original home.

This reasoning, however, does not apply to the situation in the Cleomoideae. A comparison of this distribution map with some generalized climatic maps will reveal

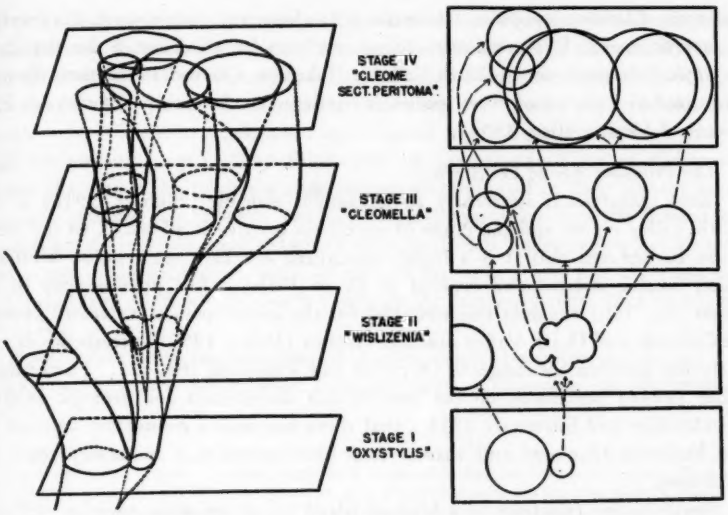

Fig. 14. Hypothetical scheme showing stages in the geographic evolution of genera as exemplified by the four genera of western North American Cleomoideae. Explanation in text.

that the primitive *Cleome* usually occurs in more mesic regions and that the ranges of *Cleomella, Wislizenia,* and *Oxystylis* are progressively more restricted to regions of greater aridity.

Since only those plants adapted to aridity were selected, the plants with "mesic" genes tended to be eliminated by progressively more arid environments. By the time such a highly modified plant as *Oxystylis* had been produced by the narrow channels of selection, its genotype had been shorn of all but "super-xeric" genes, producing a homogenic species (Stebbins, 1942). Its range is small, not because of the limited time in which its seeds could have been disseminated, but because of its narrow physiological tolerances. Selection produced a highly specialized plant, not only morphologically but physiologically and ecologically. Plants of *Oxystylis*, being biotypically poor, are literally the "prisoners" of their own genes. This is also true of the other genera, but less so. Most species of *Cleome* sect. PERITOMA are widespread but they have their limits, for none are native in the moister, wooded regions east of the Mississippi. In general, morphological conservatism is matched by relatively great physiological (ecological) tolerance; morphological specialization by physiological intolerance (specialization).[17] This statement applies to the over-all generic ranges as well as to specific ranges; thus, the most highly special-

[17] At least "immediately" following the evolution of the particular morphological specialization. That readaptation to mesic environment with retention of morphological specializations could follow, seems reasonable and has been discussed by Stebbins (1952).

ized taxa, *Cleome sparsifolia*, *Cleomella obtusifolia* var. *taurocranos*, *C. brevipes*, *C. parviflora*, etc., *Wislizenia refracta* var. *melilotoides*, all occur in the vicinity of *Oxystylis* (although not in Death Valley). Likewise, *Cleomella mexicana*, the most specialized of a phylad of three species, is restricted to the vicinity of two salt lakes in central Mexico (Iltis, 1956).

3. *The Probable Age of Oxystylis.*—

Since *Oxystylis* is apparently an indigenous endemic (Sinnott, 1916) of the Death Valley region and the range of its closest relative is allopatric to the south, it can be deduced that it is a highly specialized northern segment of *Wislizenia* which became isolated and *evolved in Death Valley*. The physiography of the region (fig. 13D) suggests this strongly, for the contemporary watershed between the Colorado and Death Valley drainage systems (Miller, 1950) corresponds exactly to the line between the ranges of *Oxystylis* and *Wislizenia* (fig. 12). Furthermore, Miller (1946) postulates, on the basis of fish distribution and geologic evidence (Blackwelder and Ellsworth, 1934), that there was once a connection between the two basins in that area and that it may have served as a migratory route for *Wislizenia*.

Death Valley functions as a kind of island whose isolation, together with the extreme climatic conditions, evidently furthered speciation. This is supported by the considerable number of endemic taxa known from there, both plants (Munz, 1935; Dressler, 1954; Tryon, 1955 [*Selaginella leucobryoides*]) and animals (Miller, 1950), which appear to be indigenous endemics usually with southern affinities that *evolved* from relics of once more widely distributed taxa (apparently not plain relics as Miller states). Living in that region, they must be adapted to its *present-day* climate of extreme heat and drought. If these adaptations originated *in situ*, they are probably recent, since, as Parish (1930) phrases it, Death Valley and the Mojave Desert had once a "greener youth," for "there is abundant evidence that in the Pleistocene Age, perhaps 20,000 years ago, this whole region enjoyed an abundant rainfall, and—as a necessary sequence—must have had vegetation very different in its character from that which prevails today." Many authors (Campbell and Campbell, 1937; Antevs, 1937; Miller, 1946; Hubbs and Miller, 1948) present strong evidence that the whole region of eastern California was one of large, deep lakes in the late Pleistocene or even more recently. Blackwelder and Ellsworth (1934) think that an immense Pleistocene lake filled Death Valley, whose waters overflowed to the south into troughs that eventually emptied into the Colorado River. Miller (1946) names the integrated river system of that time the "Death Valley system" because the Death Valley formed the sump for its waters. According to Antevs, the lakes probably date from the last pluvial period, between 20,000 and 25,000 years ago, and Lake Mojave may have been at its fullest as late as 15,000 years ago. Indians then lived in this region (Campbell and Campbell, 1937, and others in same symposium) which, in its aridity and alkalinity, is now desolate and forbidding to human habitation.

It is unlikely that *Oxystylis*, or its ancestral forms similar to *Wislizenia*, were able to grow in Death Valley during this moister period! It is also unlikely that *Oxystylis* or its ancestors migrated to Death Valley from other places than those to the south, since the northern regions were then even cooler and moister than they are now. There is furthermore no evidence that *Oxystylis* has ever grown outside its present range. "The distribution of the existing Flora of California indicates that the majority of the endemic species originated in their present area" (Campbell and Wiggins, 1947). Instead, we might postulate that the *Wislizenia*-like ancestor of *Oxystylis* migrated north *after* the Death Valley region had become about as arid as the habitats in which *Wislizenia* grows now and that the evolution of *Oxystylis took place within Death Valley in the extremely short time of 15,000 years or less.*

Fifteen millenia for the evolution of a genus seems short indeed, even for the evolution of a species under most circumstances! According to Mangelsdorf (1952):

> Evolution is usually regarded as a process which moves with majestic and unhurried pace through geological periods . . . whose progress is measured in millions of years . . . and which . . . is ordinarily thought of as so slow that even the second hand on the evolutionary clock does not travel perceptibly in the span of a human lifetime or, in many cases, during the period of recorded human history.

In some areas and in some taxa the "evolutionary clock" has practically stood still for a tremendous time span as, for example, in the temperate mesophytic wooded regions of the southeastern United States and eastern China. In many genera, the differentiations that have occurred there since the late Eocene or Miocene, 30 million or more years ago, have been on specific, varietal or even lower levels (Cain, 1943; Sharp, 1951; Li, 1952). Yet, as Mangelsdorf and others find exception to this condition in the very rapid evolution of animals and plants under domestication, we may postulate exceptions in organisms, particularly annual plants, which live in arid environments or which find themselves in environments changing rapidly toward aridity.[18]

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[18] Xerophytic and cultivated plants have certain similarities as to environment and evolution. Both occur frequently in full sunlight and in mineral soils. Both are often annuals, in which evolution has been most rapid. Both favor open habitats with little inter-specific competition. For cultivated annuals, the habitat is kept open artificially by weeding and plowing. In annual xerophytes, the habitat is also open in the sense that: (1) a desert wash or playa is often disturbed and disrupted naturally, with bare gravel and sand a result of sporadic periodic hard floods; and (2) annuals being the characteristic plants of a desert, their habitat is not closed or preempted at the beginning of the growing season by plants already there, as in a sedge meadow or forest which has a very high number of vegetatively reproduced perennials. Thus the amount of successful germinations in deserts is often very great in a good season, the nearly pure patches of certain species resembling those of cultivated plants. As in a field of cultigens where lack of interspecific competition is conducive to the survival of all genotypes planted, so in a good season the mutants as well as the standard forms of desert annuals are apt to survive, while in a dry unfavorable season those "odd" morphological types better adapted for germination requirements will be selected for and will predominate. This phenomenon may be compared to the practice of taking two heads of wheat out of 10,000 to start a whole strain, which partly accounts for the rapid evolution of cultigens. The desert environment, which periodically allows only a few favored seeds to grow in an open habitat, may appreciably alter the genetic constitution of a population in a few generations, thereby accelerating the evolutionary rate.

4. *Arid Environment and Rapid Evolution.*—

That dry and hot environments favor more rapid evolution than do mesophytic organisms, for example, has been substantiated by studies on fossil and recent organisms as well as on theoretical grounds (Muller, 1942, and Stebbins, 1947, 1949, for plants; Miller, 1950, for fishes of desert hot springs). This seems to be due to the following factors (Stebbins, 1952): (1) Ecological fragmentation of habitats, and therefore populations, in arid regions is much more pronounced than in mesic ones, thus producing many situations favoring isolation and consequently speciation. With climatic fluctuations one can expect rapidly changing selection, and with the remerging of habitats and populations, introgression. (2) The fragmentation of the habitats produces large or medium-sized populations with isolated subunits interchanging genes only occasionally, a situation most favorable to genetic drift and therefore to rapid evolution. (3) The number of special adaptive structures that can be produced in these environments may be, and often is, very large; (4) the selective pressures are very high because of the extreme climate; and (5), in annuals only, the brevity of the life cycle and the rapid multiplication of generations would increase the evolutionary rate (Sinnott, 1916).

A factor not mentioned by Stebbins, but discussed for fishes by Miller (1950), is the increase in mutation rate due to direct influence of heat. Very little experimental evidence is available on this subject. Navashin (ex Babcock, 1947) reported that the mutation rate in resting seeds of *Crepis tectorum* was accelerated by increased temperatures. Shkvarnikov and Navashin (1934) found that when resting seeds of *C. tectorum* were exposed to temperatures of 54° to 55° C. for 20 to 44 days, the surviving seedlings showed chromosomal abnormalities, particularly translocations, and an increase in the mutation rate. They call attention to the fact that since heat is widely distributed in the world, it may play a considerable role in the production of mutations; and that resting seeds are often exposed to temperatures equal to or higher than those used in their experiments. This work is not mentioned in "Temperature and Evolution" (Plough, 1942, and others in same symposium) which summarizes evidence, mainly from *Drosophila*, that high temperatures (Muller 1928, 1942), as well as temperature shocks (a distinct phenomenon!), increase mutation rates. Fankhauser (1942), working with *Triturus*, showed that extreme temperatures in the laboratory induce polyploidy, and he suggested that heat might produce polyploid individuals in nature.

That resting seeds of Cleomoideae, particularly *Oxystylis*, are exposed to extreme heat is evident, considering that Death Valley shade temperatures may be as high as 134° F. and soil temperatures certainly much over 160° F. Temperature shocks may be provided in the tremendous diurnal fluctuations which, because of low humidity, are rather typical of deserts.

Miller (1946, 1948, 1950) studied the effects of desert habitats on the evolution of Death Valley fishes. He concluded that if Lake Manly (the Pleistocene Death Valley lake) was correlated with the Tahoe stage of glaciation as postulated by

Blackwelder, the two Death Valley sibling species of *Cyprinodon*, now separated by 75 miles but originally of common ancestry, have probably been isolated for about 20,000 years. These two species live in comparatively stable habitats and are not exposed to as great fluctuations and extremes of temperature as land plants, yet they differentiated specifically in only 20,000 years. He believes (1950) that in warm spring populations, high temperatures accelerate the time rate of evolution by increasing the mutation rate as well as the number of generations per year. Although he deals with fish, his evidence seems compatible with this study.

5. *Relative Age of Genera and Relative Rates of Evolution.*—

Evidence from morphology, distribution, etc. all point to the relatively old age of *Cleome* sect. PERITOMA and the progressively greater youth of *Cleomella*, *Wislizenia*, and *Oxystylis*. The phyletic divergence of *Cleomella* from PERITOMA must therefore date further back than that of *Wislizenia* does from *Cleomella*, which in turn must have occurred before the divergence of *Oxystylis* from *Wislizenia*. If we assume in the evolution of each genus an equal evolutionary rate (an uncalled-for assumption!), we would expect (fig. 15A) the greatest morphological gap between the genera separated for the longest time (*Cleome* and *Cleomella*) and minor morphological differences between the genera which had diverged most recently (*Wislizenia* and *Oxystylis*).

The situation is, however, exactly the reverse! Inter-generic differences are greatest between *Wislizenia* and *Oxystylis*, and only very slight between *Cleome* and *Cleomella*. The relative morphological discontinuities between the genera were found to be about 2 to 3 points between *Cleome* and *Cleomella*, about 5 points between *Cleomella* and *Wislizenia*, and 7 or more points between *Wislizenia* and *Oxystylis* (fig 15B). Evidently, over-all rates of evolution were *not* uniform, but increased with the formation of each new genus. *Cleomella* evolved relatively slowly, *Wislizenia* faster, and *Oxystylis* most rapidly.[19]

This "speeding-up effect" of arid habitats on evolution is consistent with the generalizations of Stebbins (1947); namely, that "rapid evolution requires: (1) the presence of a rapidly changing environment" and (2) a group of plants "preadapted in the direction of the secular change". Both of these conditions seem to apply here. Since the four genera of Cleomoideae evolved in the arid and semi-arid regions of southwestern North America, the ancestral PERITOMA branch of *Cleome* must have been preadapted to xerophytism. We also know that during the past

[19] One of the obvious and perhaps insurmountable objections to this interpretation is simply that the gap between *Wislizenia* and *Oxystylis* is great because intermediate taxa have died out. It seems more reasonable to argue for the extinction of older taxa than for that of more recent ones, since the older the taxon the greater the opportunity for extinction. However, between the oldest taxa, *Cleome* and *Cleomella*, there are only the weakest of differences and between the youngest, the most pronounced in the subfamily.

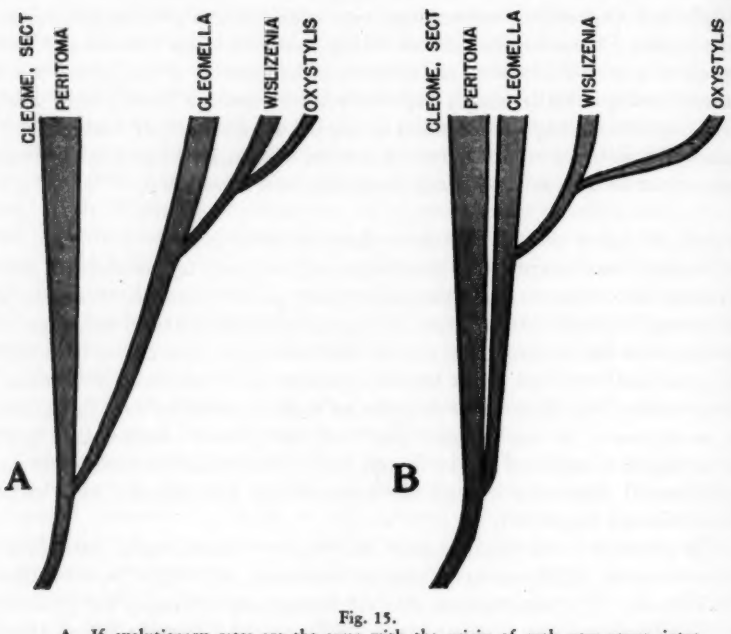

Fig. 15.

A. If evolutionary rates are the same with the origin of each new genus, inter-generic gaps would be expected to decrease from most primitive to specialized (from oldest to youngest) genus.

B. Inter-generic gaps as they occur in the western North American Cleomoideae. Note that the putative evolutionary rate is proportional to the angle between the phyletic lines.

20 million years the climate in the Southwest has oscillated tremendously from moister, subtropical in the Lower Oligocene (Chaney and Sanborn, 1933) to the initiation and development of drier and cooler grassland and desert environments of subcontinental extent. This trend progressed, with fluctuations, from warm and mild climates in the middle Pliocene (Axelrod, 1948) to the present day, except for marked interruptions during the Pleistocene, when climatic zones shifted alternately south during glacial periods and moved north during the interglacials. Since the last glacial period the change toward greater aridity has been rapid in such places as Death Valley and the Great Basin (Hubbs and Miller, 1948). This aridity is in part a result of rain shadows due to mountain building, some of which occurred as late as the Pleistocene and may be continuing today (cf. Deevey, 1949).

Cleome sect. PERITOMA may have originated during the second major burst of angiosperm evolution (Stebbins, 1947) in the middle Tertiary in the wake of climatic shifts toward aridity, either from Madro-tertiary forms that evolved in the

Mexican Plateau and moved northward, *or* from mesophytic, forest-inhabiting Cleomoideae which were left behind in the southward movement of the vegetational zones. *Cleomella,* judging from its scattered distribution in the Great Basin and east and south of the Rocky Mountains, might have had its origins also during that period. It apparently originated far east of the Sierras before their elevation in the late Pliocene, for only one of its taxa was able to reach and cross that mountain range (a putative "*pre-Wislizenia*", into western Sonora). "At the close of the Pliocene and the beginning of the Quaternary the present desert had its origin in the rain shadow resulting from the structural differentiation of the Sierra Madre-San Bernardino chain." (Cain, 1943). The ancestral "*pre-Wislizenia*", isolated from its relatives in *Cleomella* by a rising Sierra Madre, evolved into *Wislizenia,* eventually to spread north and east around the tip of the Sierra Madre, probably during and after the Pleistocene. During the glacial periods the less specialized species of *Cleome* and *Cleomella,* judging from their present great altitudinal and habitat tolerances, very likely were able to survive in approximately the same regions they occupy today; *Wislizenia* was probably restricted, as it is today, farther to the south. With the post-Pleistocene changes toward extreme aridity, the opening-up of alkaline valley floors to plant colonization and the correlated great disruption of previously existing habitats, we can postulate a northward expansion of ranges of xerophytes and an evolution that filled some of the newly available niches by producing not only *Oxystylis* in Death Valley, but also such exceedingly specialized species as *Cleomella brevipes* in the Mohave Desert, *Cleome sparsifolia* in Nevada, and the local diversification of *Wislizenia* and other species of *Cleomella.*

"Accelerative evolution" is interpretable through organism-environment relationships as postulated by Simpson (1944) and Stebbins (1949, 1950); in our case, through the obvious direct relationship of morphological specialization to habitat specialization and to evolutionary rate. We might say that mild environment would result in mild selection, the consequence of which is slow morphological or physiological evolution; a change to a progressively more arid environment would produce greater selection, resulting in faster evolution. Accelerative evolution, then, will be exhibited by semi-desert plants, or plants preadapted to arid environments, evolving into progressively better-adapted types which are able to invade (or survive in) progressively more arid regions. The result would be increased selection, mutation, etc., making invasions of still more specialized habitats possible, which in turn would intensify the processes that have been outlined.[20]

Deserts and desert evolution must have occurred on the earth for a long time. If there is one definite fact we know concerning the world's geologic past, it is that mountain ranges have formed only to be worn down and to be replaced by new chains. That mountain ranges once had rain shadows with deserts as they do today is a warranted assumption, as is the former presence of subtropical

[20] Whether this applies generally I do not know. The steady increase in body size of the American Equids as illustrated in Romer (1949) is essentially an accelerative increase, both for the *Megobippus* as well as the *Equus* line.

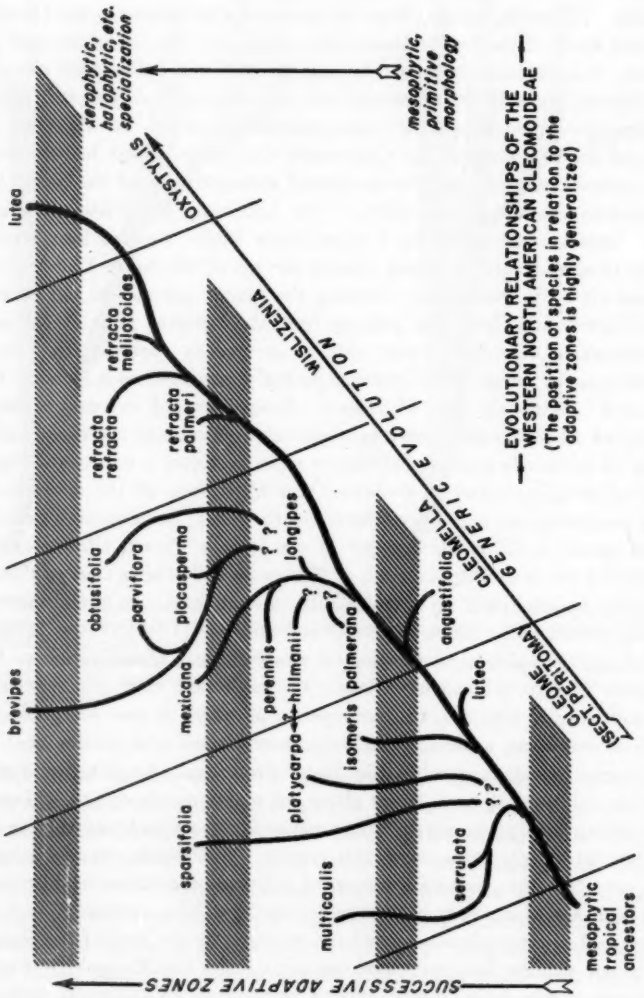
xerophytic, halophytic, etc. specialization
mesophytic, primitive morphology
EVOLUTIONARY RELATIONSHIPS OF THE WESTERN NORTH AMERICAN CLEOMOIDEAE
(The position of species in relation to the adaptive zones is highly generalized)
OXYSTYLIS
WISLIZENIA
CLEOMELLA
GENERIC EVOLUTION
CLEOME (SECT. PERITOMA)
lutea
refracta mellilotoides
refracta refracta
refracta palmeri
obtusifolia
parviflora
plocasperma
longipes
brevipes
mexicana
perennis
hillmanii
palmeriana
angustifolia
lutea
isomeris
platycarpa
sparsifolia
multicaulis
serrulata
mesophytic tropical ancestors
SUCCESSIVE ADAPTIVE ZONES

Figure 16

high pressure belts and their resultant arid zones. The high speed of evolution in deserts may therefore explain the problems of "macro-evolution" of the paleontologists and the seemingly sudden origin of phyletic groups from morphological types so different that they cannot be recognized by us as ancestral. This is particularly true if we assume that with reverse changes toward milder climates, rapid evolution in deserts may be followed by a reverse and slower change toward mesophytism. In some instances the "new" types of organs developed as desert adaptations may have had, by change in function and by some readjustment of structures, superior survival value to other, more ancient mesophytes. That organisms may take the circular route from mesophytism to xerophytism back to mesophytism has been documented by Stebbins (1952), and certainly has occurred again and again, in the larger sense, in the evolution of major divisions of the plant and animal kingdoms ("mesophytic" fish to "xerophytic" terrestrial quadruped to "mesophytic" whale, etc.). The general significance of such possibilities in the more recent evolutionary history of angiosperms[21] has not been fully appreciated by most evolutionists. All desert evolution was not necessarily dead end!

VIII. Summary

The four genera of western North American Cleomoideae (Capparidaceae) can be arranged in a remarkably complete phyletic reduction series, from the primitive *Cleome* sect. PERITOMA (6 spp.) through the progressively more specialized *Cleomella* (10 spp.) and *Wislizenia* (1 sp. with 3 vars.) to the highly specialized *Oxystylis* (1 sp.). The reductions run from many-seeded siliques through few-seeded silicules to two-seeded schizocarps; from open, bracteate racemes through denser, ebracteate ones to congested, ebracteate raceme-clusters; from small to very complex stipules; and from plants with much vegetative growth and delayed flowering to ones in which even the earliest leaves subtend flowers or racemes. Nearly all these reductions are interpretable as adaptive modifications, a result of selection by arid environments which favored plants with more rapid or economical life cycles.

The geographic distributions also imply that these reductions and specializations are due to adaptive evolution. The primitive forms are widely distributed in more mesic climates; the specialized have progressively smaller, essentially equiformal areas centering about the Death Valley region of California and Nevada, where *Oxystylis* is endemic. The ranges and degrees of relationship of individual taxa within each genus follow patterns corresponding to their morphology. The taxa of the primitive (therefore oldest) genus *Cleome* are all more or less sympatric

[21] In the known fossil record, there are almost no "protoangiosperms", or even primitive ancestors, of any of the present-day angiosperm families. Angiospermy, our major phylogenetic puzzle, may perhaps be explainable as an adaptation to xerophytic life. If this be true, the lack of fossil remains might be due to extremely rapid (geologically "instantaneous") desert evolution, with the consequent short span in which widespread fossilization might have taken place, as well as the reduced opportunities for fossilization characteristic of desert habitats (in contrast to mesic or hydric habitats).

and sharply distinct, those of the more specialized genus *Cleomella* both allopatric and sympatric and less sharply distinct, and those of the monotypic, polymorphic *Wislizenia* allopatric with closely related populations. The most specialized, and therefore youngest genus *Oxystylis* is monotypic and monomorphic. The fact that there are different kinds of genera can in part be explained by differences in their age. In evolution through geographic isolation, taxa of a genus have to be allopatric before they can become sympatric, and by studying their geographic ranges and the amount of sympatry or allopatry, we can correlate geographical distribution with morphology and variability, and determine the relative age of a genus.

By extending "Jordan's law" not only to apply to the most closely related taxa within a genus, but also to a pair of monotypic genera or to the two most closely related species of two related genera, we can determine (if evolution has been geographic and sufficiently recent) the geographic direction of evolution by deciding which of the two taxa is the most primitive. Thus, *Cleome* sect. PERITOMA originated from primitive tropical species allopatric to the south. The primitive species of *Cleomella* seem to have originated from a primitive *Cleome* allopatric to the northwest. The primitive variety of *Wislizenia* is allopatric to the west of, and separated by the Sierra Madre Occidental from its putative ancestor in *Cleomella*. Finally, the most specialized variety of *Wislizenia* and its offspring *Oxystylis* have exactly allopatric ranges, the dividing line being the Death Valley basin-Colorado River basin watershed.

Since the Death Valley basin contained a series of tremendous post-Pleistocene lakes about 15,000 years ago, it seems very unlikely that *Oxystylis* migrated to Death Valley except in the form of a "*Wislizenia*-like" plant *after* a desert or semi-desert climate had become established; it is postulated therefore that *Oxystylis evolved* (1) *in the Death Valley area* (2) *within the extremely short time of 15,000 years or less*. That generic evolution at such a tremendous speed is possible under extreme selection is amply illustrated by domesticated organisms, plants and animals. Furthermore, there is a great similarity between the habitat and evolutionary rate of cultivated annuals and desert annuals. In *Oxystylis*, the rapid changes towards greater aridity resulted in extreme selection which, together with other factors characteristic of deserts, is postulated to have been responsible for this rapid evolution. To the four factors (Stebbins, 1952) which help make "aridity a stimulus to plant evolution," a fifth, the effect of extreme temperatures on the mutation rate, may be added.

The increasing inter-generic discontinuities between the four genera, represented by the arbitrary numbers 3–5–7, point to an accelerative increase in the speed of evolution with the development of each new genus. The "accelerative evolution" may be explained by an extension of Simpson's and Stebbins' postulates that in preadapted organisms, the more stringent the environment, the faster evolution, which in turn would produce better-adapted organisms able to survive in, or invade, still more stringent environments with still greater selection.

The very rapid evolution in deserts may have been of major evolutionary importance in creating radically new morphological types. With a return to mesophytic climates, some of these types may have been highly successful. Perhaps some precursors of the angiosperms, whose ancestors are as yet unknown, had their origin in desert evolution.

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STYLITES, A NEW GENUS OF ISOETACEAE

ERIKA AMSTUTZ[1]

Stylites andicola E. Amstutz, gen. et spec. nov. Isoetacearum.

Plantae amphibiae vel subamphibiae in societatibus dense caespitosis supra margines paludum alpinorum frequentes. Caudices maximi crassi apice profunde bilobi usque 7 cm. longi 1.2 cm. lati vel ultra; cortice crassiusculo fusco cicatricibus foliorum vetustorum notato; radicibus per longitudinem uno latere caudicis valde secundis usque fere 5 mm. crassis speciminum nostrorum simplicibus fortasse tandem dichotomis. Folia in rosulis densissime imbricata oblongo-lanceolata apice anguste caudato-acuminata ibique valde reflexa ca. 5.0–5.5 cm. longa 5–8 mm. lata crassa margine partis basalis aut vaginae late hyalino medio et parte apicale grosse bullato. Sporangia usque 1.5 cm. supra basem foliorum instructa oblonga ca. 5 mm. longa 2 mm. lata e foveola tenue margine indistincto proventa; trabeculis paucis paxilliformibus; velo nullo; macrosporis albidis laevibus magnitudine aliquantulum dissimilibus ca. 428–643 μ latis; microsporis non visis. Ligula anguste cordato-triangularis 3–5 mm. longa. — Nomen e στυλίτης habitore in columna derivatur caudice notabili designans.

PERU: Depto. Lima, Prov. Huarochiri, above Casapalca near Caprichosa, in alpine bogs, alt. 4750 m., 2 July, 1956, *E. Amstutz 2000* (Herb. Missouri Bot. Gard., HOLOTYPE).

These curious plants were found on a moist and limy substrate around the boggy margins of a small glacial lake near Caprichosa, a few kilometers from Casapalca, central Peru, at an elevation of 4750 m. The plants live in extremely crowded colonies forming flat and dense cushions in a belt 2–3 m. broad and about 3–5 m. from the waters of the lake. The largest colonies consist of 40 or more individual plants. Better developed specimens were found in the peripheral parts of the larger cushions (50–60 cm. in diameter).

The plants apparently are well adapted to their environment. The leaves and upper portions of the caudices are aerial, but so crowded that considerable protection from the severe environment is effected. Associates of *Stylites andicola* are sods of peat and swamp bryophyta, convex and very hard cushions of *Distichа muscoides* (Juncaceae), tufts of *Calamagrostis chrysantha* (Gramineae), etc.

These plants display several innovations which deviate significantly from the very conservative architecture of all known species of *Isoetes*. The elongate caudices are outstanding; furthermore, in digging my specimens in the frozen soil, I unfortunately failed to obtain unbroken plants, and it seems possible that the

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dense cushions may actually be formed through branching of the caudices of single plants, at least in part. The fleshy roots are borne along only one side of each caudex. Here, also, my excavation was not sufficiently careful, for all of the roots were cut during the process. However, in all attached roots which remain, some more than a decimeter in length, no branching may be seen. The short broad leaves with thick and recurved tips, to which effective photosynthesis appears to be restricted, are most exceptional; but most remarkable of all is the attachment of the sporangia far above the base of the sporophylls. The fovea is extremely shallow and the sporangium is less than half included within it. The trabeculae are few and peg-like. Unfortunately, microsporangia were not observed.

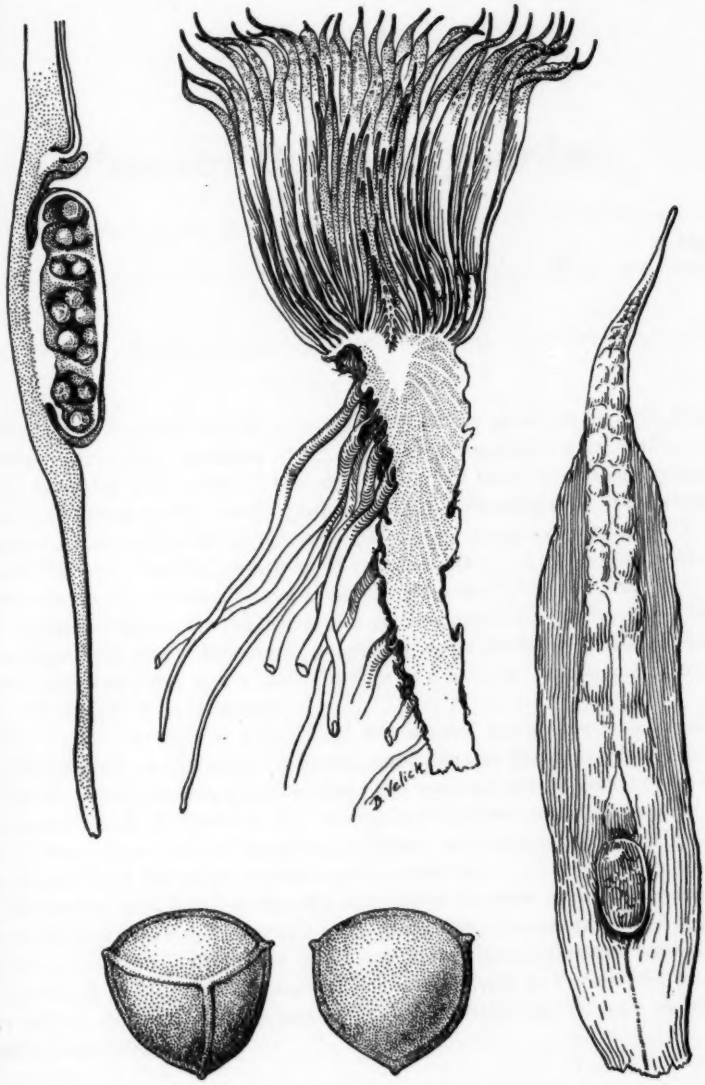

Figure 1. *Stylites andicola*